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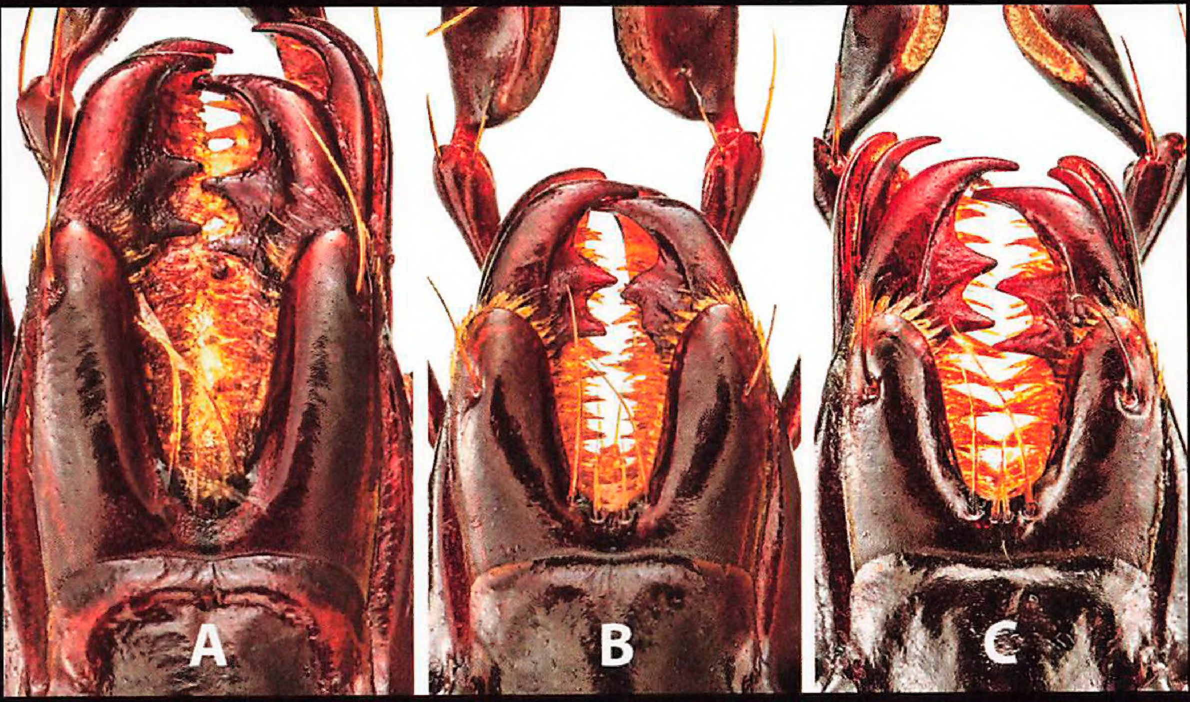

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Institute for Biodiversity Science & Sustainability

CALIFORNIA ACADEMY OF SCIENCES

COVER IMAGES

FRONT COVER: Figure 5 in LaBonte & Kavanaugh, p. 308: Labrum, dorsal view.
A. *Scaphinotus mannii* Wickham (Steptoe Canyon, Whitman County, Washington);
B. *S. regularis* (LeConte) (9 km SSE of Lowell, Idaho County, Idaho);
C. *S. relictus* (Horn) (8 km SE of Craigmont, Lewis County, Idaho).

COVER DESIGN

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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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New Synonymy in the Afrotropical *Tachytes* Panzer, 1806 (Hymenoptera: Crabronidae)

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Tachytes mirus **and** ***Tachytes observabilis*****, described by Kohl in the same paper in 1894, are recognized as being two sexes of one species.** ***Tachytes mirus*** **is here selected as a valid name, and** ***Tachytes observabilis*** **as its junior synonym.** ***Tachytes rhodesianus*** **Bischoff, 1913, and** ***T. midas*** **Arnold, 1929, are newly synonymized with** ***T. pulchrivestitus*** **Cameron, 1908, a species resurrected from synonymy with** ***T. mirus*** **Kohl. The status of** ***Tachytes nigroannulatus*** **as valid species is confirmed. Diagnostic characters are provided for** ***T. mirus*****,** ***T. nigroannulatus*****, and** ***T. pulchrivestitus*****.**

My studies of the Afrotropical *Tachytes* revealed three unnoticed synonymies discussed below, two of which have been confirmed by the study of respective holotypes. The greatest part of the material examined belong to the California Academy of Sciences, but important specimens (including types) are deposited in the following institutions (the abbreviation preceding their names are used in the text):

NHMW: Naturhistorisches Museum, Wien, Austria (Dominique Zimmermann).

NHRM: Naturhistoriska riksmuseet, Stockholm, Sweden (Hege Vårdal).

SAM: Iziko Museum of South Africa, Cape Town, South Africa, formerly South African Museum (Simon van Noort, Aisha Mayekiso).

TMP: Ditsong National Museum of Natural History, Pretoria, South Africa, formerly Transvaal Museum.

ZMHU: Museum für Naturkunde, Berlin, Germany, formerly Zoologisches Museum der Humboldt Universität (Viola Richter).

Tachytes mirus Kohl

Tachytes mirus Kohl, 1894:295, ♀ (as *mira*, incorrect original termination). Holotype or syntypes: ♀, Mozambique: Delagoa Bay, now Maputo Bay (TMP), not seen. – Dalla Torre, 1897:691 (in catalog of world Hymenoptera); nec R. Turner, 1916:445 and 1917d:11 (= *Tachytes danae*); Arnold, 1923a:188 (similar to *Tachytes observabilis*), 1930:4 (in checklist of Afrotropical Sphecidae); Berland, 1942:3 (Central African Republic: Fort Sibut); van Vondel, 1995:25 (specimens from Malawi in Natuurmuseum Rotterdam). – **As *Tachytes mirus***: R. Bohart and Menke, 1976:266 (in checklist of world Sphecidae).

Tachytes observabilis Kohl, 1894:295, ♂. Holotype or syntypes: ♂, Tanzania: Zanzibar: no specific locality (TMP), not seen. **New synonym.** – Dalla Torre, 1897:692 (in catalog of world Hymenoptera); R. Turner, 1917:12 (in revision of Afrotropical *Tachytes*; description of ♀; Angola, Kenya, Malawi, Uganda); Arnold, 1923a:184 (in revision of southern African *Tachytes*), 1930:4 (in checklist of Afrotropical Sphecidae); Schouteden, 1930:92 (Zaire); Arnold, 1943:79 (Zaire: Albert National Park: Bitshumbi), 1951:146 (Ethiopia: Lake Anasa); Robertson, 1969:480 (Tanzania: Urambo); R. Bohart and Menke, 1976:266 (in checklist of world Sphecidae); Seyoum and Pulawski, 2001:325 (potential control agent of acridid pests in Ethiopia); S. Gess and F. Gess, 2003:112 (Namibia: visiting flowers of *Hermbstaedtia* sp., Amaranthaceae, and *Geigeria* sp., Asteraceae).

Taxonomic History.— In his 1894 paper, Kohl described *T. mirus* from Delagoa Bay in Mozambique (based on several females), and *T. observabilis* from the Island of Zanzibar (based apparently on one male). Unfortunately, he did not pay attention to the length of the galea or to the palpal formula. Both species were recognized by R. Turner (1917) and Arnold (1923a, b) in their respective revisions of the Afrotropical *Tachytes*, but neither of the two authors suspected that they may be the two sexes of one species. Turner (1917) thought that *T. mirus* was a member of his subgenus *Calotachytes*, thus attributing it the palpal formula of 5 + 3. Arnold (who may have seen the types of both Kohl's species) described in 1923 as *Tachytes danae* the species interpreted as *T. mirus* by Turner, and treated *T. mirus* as a member of *Tachytes* s.s., with the palpal formula of 6 + 4. Turner also described the female of *T. observabilis*, and Arnold (1923) commented under *T. mirus*: "Except that the anterior metatarsus has six to seven spines [six in *T. observabilis*] and the much shorter pygidial area, there is nothing to distinguish this form from *observabilis*".

Species Identification.— The type material of both *T. mirus* and *T. observabilis* is deposited in the Ditsong National Museum of Natural History in Pretoria, South Africa, but I was not able to obtain them for examination in spite of many requests. Kohl (1994) description of these two species did not mention such an essential character as the length of the galea, but Arnold (1923) described it as being longer then the scape.

Species Recognition.— *Tachytes mirus* is a member of the *basilicus* species group which is characterized by the galea longer than the scape (Figs. 2, 3), not separated from the stipes by a sulcus, the first article of the labial palpus elongate, about as long as the scape (Fig. 3), the palpal formula 6 + 4, the clypeal median lobe broad, evenly arcuate, and in the male the least interocular distance short (Fig. 4), smaller than the distance between the ventral ends of the hindocelli.

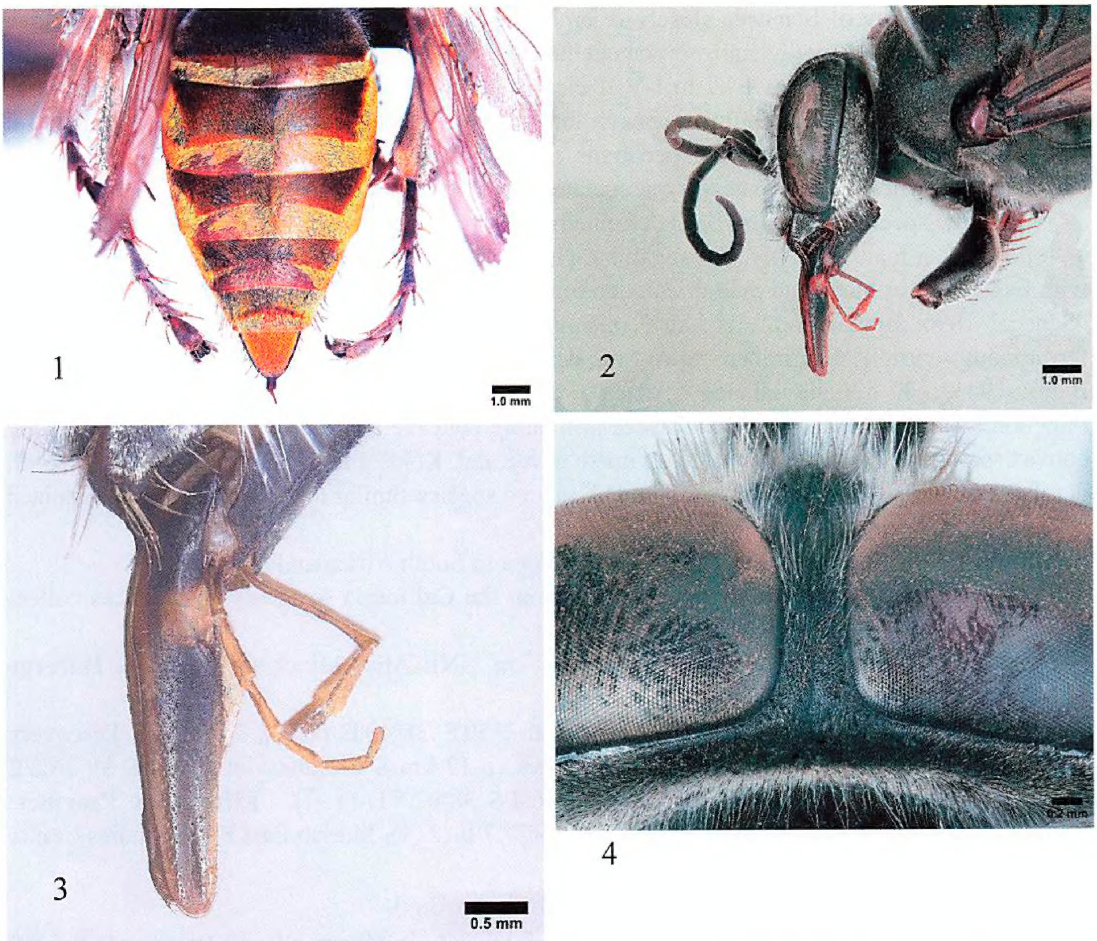
The *basilicus* species group includes the following 15 described species (all African except *T. monetarius* from India and *T. galeatus* from Madagascar): *T. abercornensis* Arnold, 1959, *T. basilicus* (Guérin-Méneville, 1844), *T. galeatus* Pulawski, 2019, *T. hamiltoni* R. Turner, 1917, *T. irritabilis* R. Turner, 1917, *T. labilis* R. Turner, 1917, *T. mirus* Kohl, 1894 (= *T. observabilis* Kohl, 1894), *T. monetarius* F. Smith, 1856, *T. neglectus* R. Turner, 1917, *T peronatus* R. Turner, 1017, *T. praestabilis* R. Turner, 1917, *T. separabilis* R. Turner, 1917, *T. simulatrix* R. Turner, 1917, and *T. velox* F. Smith, 1856 (I studied all Arnold's, F. Smith's, and R. Turner's types in the Natural History Museum, London back in 1974, and took detailed notes on them). Most of them have silvery, apical fasciae on terga I-IV or I-V, and only in the following six are the gastral setae all golden, arranged in a checkered pattern (Fig. 1): *T. abercornensis*, *T. basilicus*, *T. mirus*, *T. monetarius*, *T. peronatus*, and *T. velox*. They differ from *T. mirus* as follows:

In the male of *T. abercornensis* (the female is unknown), flagellomeres II-VII are slightly concave dorsally and slightly convex ventrally, and all sterna are covered with dense, erect setae, whereas in the male of *T. mirus* the flagellum is cylindrical and most of sterna III-V are either glabrous or covered with appressed setae (only apical depressions mesally are covered with suberect setae).

In *T. basilicus* the gaster is ferruginous, the scutum has appressed, silvery setae at least in the anterolateral corner, and in the female the punctures of the pygidial plate are somewhat sparser, the setae not entirely concealing the integument. In *T. mirus* the gaster is black (as are the flagellum and the legs), the appressed, silvery setae are absent from the scutum, and in the female the punctures of the pygidial plate are denser, the setae entirely concealing the integument.

In *T. monetarius*, the forewing is darkened along the anterior margin (the dark area varying in intensity, and also in length, either extending to the apex of the marginal cell, or ending at the cell's base). In *T. mirus*, the wings are uniformly clear, somewhat darkened only along the apical margin.

In the male of *T. peronatus* (the female is unknown), sternum VIII is emarginate apically, and



FIGURES 1–4. *Tachytes mirus*: 1: female gaster dorsally; 2: female head in lateral view showing elongate galea; 3: female galea in lateral view; 4: male vertex in dorsal view.

the midbasitarsus has short spines ventrally. In the male of *T. mirus*, sternum VIII is rounded apically, and the midbasitarsus has no spines on venter.

In *T. velox*, sternum II has large, sparse punctures, and it is largely glabrous in the male; the male midbasitarsus is slightly dilated apically, the dilated part well separated from the more basal area, and covered ventrally with short, suberect setae. In the female of *T. mirus*, sternum II is covered with minute, dense punctures, interspersed with somewhat larger, sparse punctures; in the male, sternum II is all covered with erect setae, the midbasitarsus has no distinct, dilated apical part and no erect setae.

JUSTIFICATION OF NEW SYNONYMY.— Many females evidently conspecific with *T. mirus*, and many males evidently conspecific with *T. observabilis*, were collected together in eight localities in Ethiopia, Kenya, Namibia, Tanzania, Zambia, and Zimbabwe (see the Records below), convincingly demonstrating that they are the opposite sexes of one species. Acting as First Reviser (Article 24.2), I hereby select *Tachytes mirus* as the valid name and *Tachytes observabilis* as its junior synonym. *Tachytes pulchrivestitus*, incorrectly regarded as a junior synonym of *T. mirus*, is actually a valid species (see below).

SIMILAR UNDESCRIBED FORMS.— Seven males from Zimbabwe and two from Namibia in the

California Academy of Sciences closely resemble *T. mirus* in having an elongate galea, golden gastral setae and an equally narrow postocellar area. They differ from *T. mirus* in having the ventral side of flagellomeres I-VI to I-VIII clearly yellowish brown, and at least flagellomeres II-VI with the dorsal surface slightly concave and the ventral surface convex. Also, the hindfemoral venter has no erect setae in the specimens from Zimbabwe. Most likely they represent an undescribed species. Unfortunately, no associated female is available.

The three specimens in NHMW determined as *T. observabilis* (examined 19 January 2019) are as follows: 1. a male from "N.W. Tanganika, Grauer, 1910", is like the males of *T. mirus* above, with flagellomeres black and cylindrical, determined "*observabilis*, det. Kohl"; 2. a female labeled "Senegal 1896, Brauer don.", is like *T. mirus* described above but with the flagellum brown ferruginous ventrally, determined "*velox* Sm., det. Kohl" and "*Tachytes observabilis* Kohl, det. P.P. Babiy 1941"; 3. a male labeled "Africa", with flagellomeres II-IX yellowish brown, and flagellomeres II-IV with the dorsal surface minimally concave and the ventral surface minimally convex (practically cylindrical), is determined "*velox*, det. Kohl" and "*Tachytes observabilis* Kohl, det. P.P. Babiy 1941". Specimens no. 2 and 3 may be species similar to *T. mirus*, but unrecognized so far.

GEOGRAPHIC DISTRIBUTION (Fig. 5).— Ethiopia to South Africa and Namibia.

RECORDS (all the specimens recorded are from the California Academy of Sciences collection).

ETHIOPIA: **Gamo Gofa Province**: 40 road km NNE Arba Minch (1 ♀, 1 ♂). **Harerge Province**: 44 km ENE Jijiga (1 ♂).

KENYA: **Coast Province**: Mount Kasigau at 3°50′S 38°40′E (1 ♂), Taita Hill Discovery Centre at 3°42.3′S 38°46.6′E (3 ♂), Tiwi Beaches ca 17 km S Mombasa at 4°14.4′S 39°36.2′E (1 ♀, 3 ♂). **Eastern Province**: Mwingi at 0°56.4′S 38°02.8′E (1 ♂). **Rift Valley Province**: Lodwar road 4 km N road to Sigor at 1°33.7′N 35°27.7′E (2 ♂), Marich Pass Field Studies Centre at 1°32.2′N 35°27.4′E (3 ♀, 11 ♂).

MOZAMBIQUE: Maputo Bay (Kohl, 1894, as Delagoa Bay).

NAMIBIA: **Oshikoto Region**: 10 km SE Tsumeb (1 ♀, 1 ♂). **Otjozondjupa Region**: 18 km NE Kalkfield at 20°45′S 16°16′E (1 ♂), 28 km NW Otjiwarongo at 20°21′S 16°27′E (1 ♂).

SOUTH AFRICA: **North West Province**: Hartiebeespoort (2 ♀).

TANZANIA: **Coast Region**: 17 km E Chalinze at 6°39.2′S 38°30.2′E (3 ♀, 4 ♂). **Iringa Region**: 18 km W Iringa at 7°53.8′S 35°35.7′E (1 ♀, 1 ♂). **Kilimanjaro Region**: 20 km SE Same at 4°05.1′S 37°53.54′E (1 ♂). **Morogoro Region**: 3 km S Mikumi at 7°25.6′S 36°59.1′E (1 ♀), 48 km W Morogoro at 6°56.9′E 37°20.2′E (1 ♂). **Zanzibar**: no specific locality (Kohl, 1894).

ZAMBIA: **Central Province**: 65 km WNW Lusaka at 15°10′S 27°25′E (1 ♂), 2 km E Mumbwa at 15°01′S 27°04′E (1 ♂), 6 km W Mumbwa at 15°02′S 27°00′E (1 ♂). **Eastern Province**: 6-18 km SW Mfuwe (1 ♀, 9 ♂), 31 km E Petauke at 14°18′S 31°36′E (5 ♂), 32 km E Petauke at 14°17′S 31°37′E (1 ♂). **Lusaka Province**: 25 km E Lusaka at 15°21′S 28°30′E (2 ♂). **Northern Province**: 60 km N Kasama at 9°42′S 31°10′E (3 ♂).

ZIMBABWE: Bulawayo airport at 20°00′S 28°38′E (1 ♀), 30 km S Harare (1 ♂), Leighwoods 52 km SW Bulawayo at 20°26′S 28°15′E (1 ♂), Lion and Cheetah Park 24 km W Harare at 17°50′S 30°49′E (4 ♂), Redbank at Kami River at 20°00′S 28°22′E (3 ♂), Victoria Falls at 17°56′S 25°50′E (1 ♀, 3 ♂).

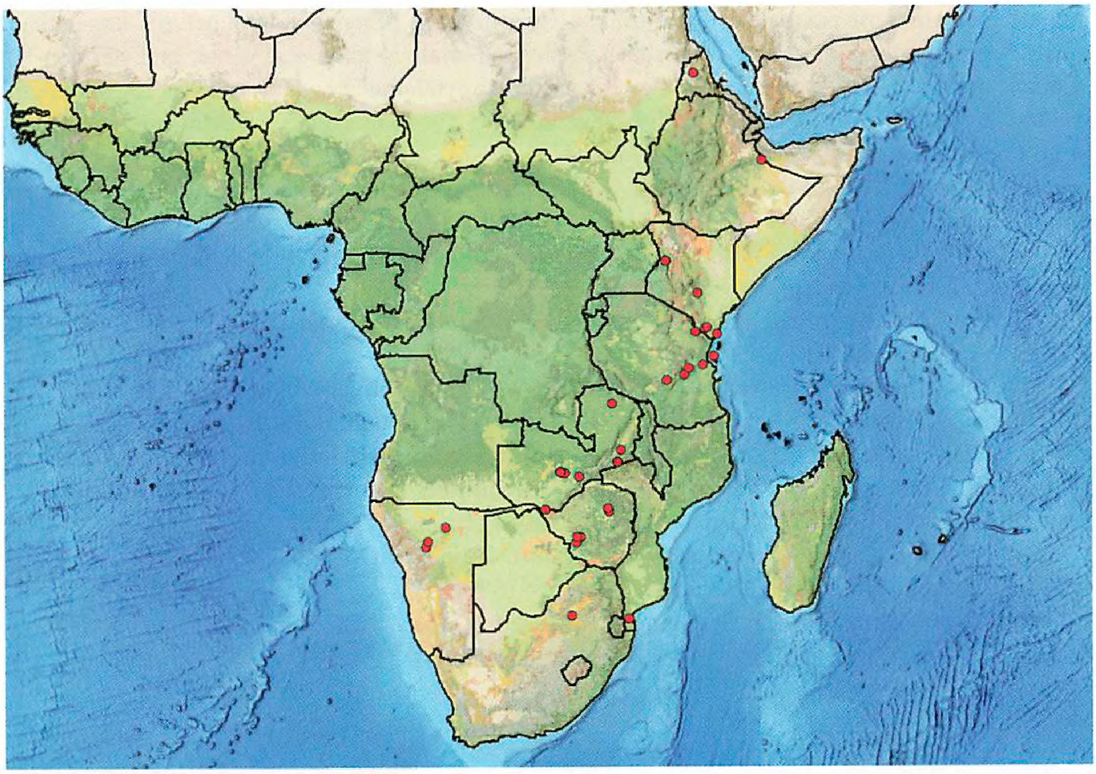


FIGURE 5. Collecting localities of *Tachytes mirus*.

Tachytes nigroannulatus Bischoff

Tachytes nigroannulatus Bischoff, 1913c:69, ♂. Holotype: ♂, Zimbabwe: Springvale (ZMHU), examined. – R. Turner, 1917:42 (in revision of Afrotropical *Tachytes*; Zimbabwe; as *nigroannulata*); Arnold, 1923a:152 (as junior synonym of *Tachysphex syriacus* Kohl, 1888 = *T. albocinctus* (Lucas, 1849)), 1927:117 (valid species), 1930:5 (in checklist of Afrotropical Sphecidae); R. Bohart and Menke, 1976:266 (in checklist of world Sphecidae).

Tachytes glabriusculus Arnold, 1923b:209, ♂ (as *glabriuscula*, incorrect original termination). Syntypes: Zimbabwe: Victoria Falls, Sawmills (SAM, TMP). Synonymized with *Tachytes nigroannulatus* by Arnold, 1927:117

NOMENCLATURAL HISTORY.— Arnold thought in 1923 that *Tachytes nigroannulatus* was a junior synonym of *Tachysphex syriacus* Kohl, 1888 (i.e., of *T. albocinctus* (Lucas, 1849)), but in 1927 and 1930 he treated it as a valid species, apparently without seeing the type. Having examined the holotype of *T. nigroannulatus* in 2019, I can confirm Arnold's opinion of 1927.

RECOGNITION CHARACTERS.— *Tachytes nigroannulatus* is a small species (female length 7.1-10.2 mm, male length 6.7-8.7 mm), with the galea about as long as wide (markedly shorter than the scape), the thorax, propodeum, and gaster black, gastral terga I-IV with silvery fasciae (setae of tergum V black), and the palpal formula 6 + 4. It differs from most of its African congeners, in particular from *T. niloticus* R. Turner, in lacking erect setae on the scape (a previously unobserved feature). *T. dilaticornis* R. Turner and *T. pygmaeus* shares this character, but both of them are very different. The first of these species has the tergal setae golden, including tergum V (among other differences), and the second differs in having the propodeal enclosure glabrous and the gaster ferruginous at least basally (among other differences). Other characters of *T. nigroannulatus*

include: punctures of postocellar area minute, close to each other (a few punctures larger than most); wing membrane hyaline; erect setae absent on female hindfemoral venter and sternum II; width of male clypeal lamella greater than distance between lamella and eye margin; dorsal length of flagellomere I 1.5-1.7 × apical width in female, 1.3-1.5 × in male. The color of hindfemur and of all tibiae varies from black to ferruginous.

GEOGRAPHIC DISTRIBUTION (Fig. 6).— *Tachytes nigroannulatus* was known from Zimbabwe only. In reality, it also occurs in Kenya, Namibia, South Africa, and Tanzania.

RECORDS (except for the holotype of *Tachytes nigroannulatus,* all the specimens recorded are from the California Academy of Sciences collection).

KENYA: **Rift Valley Province**: Marich Pass Field Studies Centre at 1°32.2′N 35°27.4′E (7 ♀, 2 ♂).

NAMIBIA: **Karibib District**: 43 km E Karibib (1 ♂), Khan River 23 km N Karibib at 21°47′S 15°57′E (1 ♀). **Kavango District**: 100 km SW Rundu (1 ♂). **Okahandja District**: Waldau River 17 km W Okahandja at 21°57′S 16°45′E (4 ♂). **Otjiwarongo District**: 3 km NE Kalkfeld (1 ♂), 18 km NE Kalkfeld at 20°45′S 16°16′E (1 ♀). **Rehoboth District**: 9 km S Rehoboth (1 ♂). **Tsumeb District**: 30 km E Namutoni (1 ♂), 10 km SE Tsumeb (3 ♂).

SOUTH AFRICA: **Free State**: Sandveld Nature Reserve at 27°40′S 25°41′E (2 ♀, 3 ♂). **Gauteng**: Pretoria Botanical Garden at 25°44′S 28°16′E (1 ♂).

TANZANIA: **Mara Region**: Seronera in Serengeti National Park (1 ♂). **Morogoro Region**:

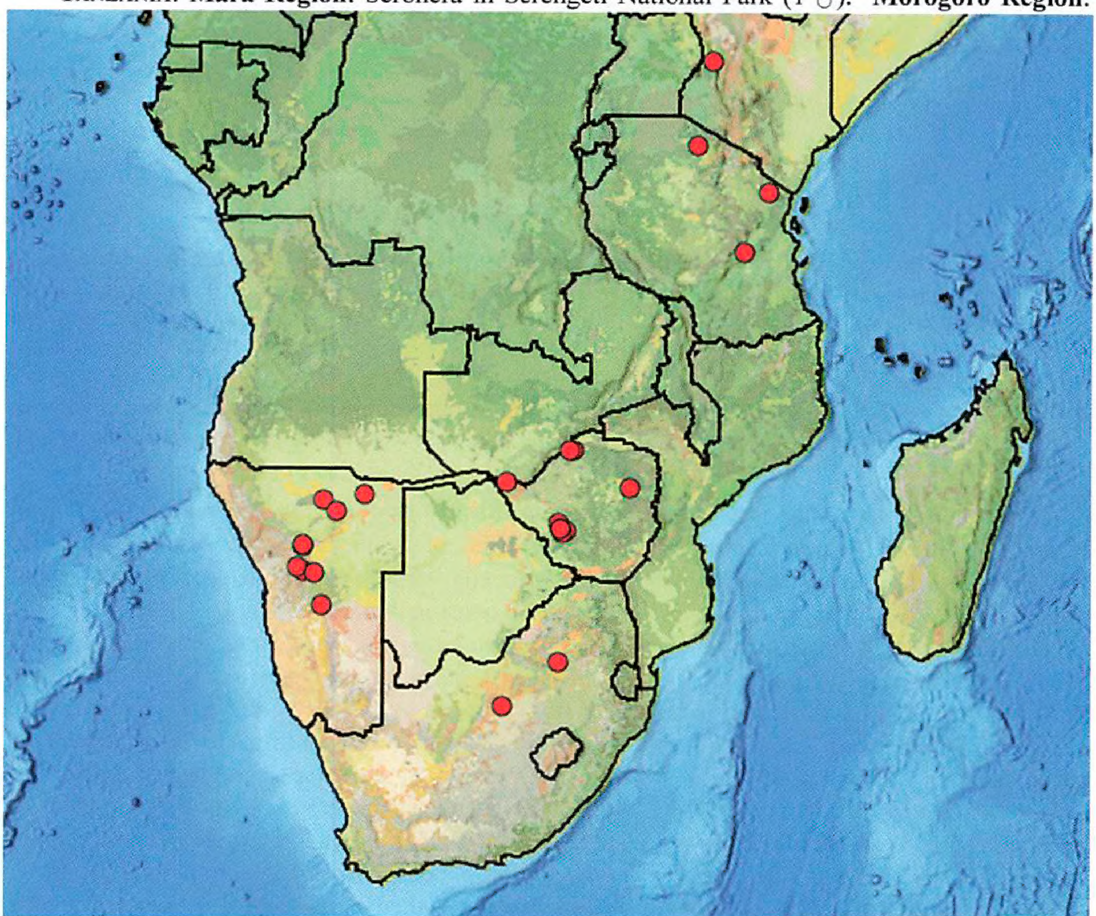


FIGURE 6. Collecting localities of *Tachytes nigroannulatus.*

3 km S Mikumi at 7°25.6′S 36°59.1′E (2 ♀, 1 ♂). **Tanga Region**: 2 km NE Mkomazi at 4°37.8′S 38°05.5′E (4 ♀).

ZIMBABWE: Bulawayo: Umguza River at 20°05′S 28°37′E (1 ♀), Charara 20 km ESE Kariba at 16°33′S 28°58′E (1 ♂), Kami (= Khami) Ruins at 20°09′S 28°26′E (1 ♀, 1 ♂), Kariba at 16°32′S 28°49′E (1 ♀, 6 ♂), 11 km NE Nyamandhlovu at 19°48′S 28°16′E (2 ♀, 1 ♂), Redbank at Kami River at 20°00′S 28°22′E (2 ♂), Sawmills at Umguza River at 19°35′S 28°02′E (1 ♀), Springvale (1 ♀, ZMHU, holotype of *Tachytes nigroannulatus*),Victoria Falls at 17°56′S 25°50′E (2 ♀, 5 ♂).

Tachytes pulchrivestitus Cameron

Tachytes pulchrivestitus Cameron, 1908:284, ♀ (as *pulchrivestita*, incorrect original termination). Holotype: ♀, Tanzania: Tanga Region: Mombo (NHRM), examined. **Here resurrected from synonymy**. – R. Turner, 1913:754 (as new synonym of *Tachytes mirus*), 1917:20 ("from the description this appears to be nearest to *T. rhodesiana*").

Tachytes rhodesianus Bischoff, 1913c:70, ♀. Holotype: ♀, Zimbabwe: Springvale (SAM), examined. **New synonym.** – R. Turner, 1917:19 (in revision of Afrotropical *Tachytes*, description of ♂, South Africa, Zimbabwe, as *rhodesiana*); Arnold, 1923:185 (in revision of southern African *Tachytes*, as *rhodesiana*), 1927:117 (females with six rather than five rake spines on forebasitarsus, as *rhodesiana*), 1929c:389 (postocellar area incorrectly described in 1923, correctly given in description of *T. midas*, as *rhodesiana*), 1930:4 (in checklist of Afrotropical Sphecidae); Berland, 1942:2 (Mali: Telimané north of Kayes; as *rhodesiana*); R. Bohart and Menke, 1976:266 (in checklist of world Sphecidae).

Tachytes midas Arnold, 1929:389, ♀, ♂. Lectotype: ♀, Zimbabwe: Bulawayo (SAM), **present designation**, examined. **New synonym.** – Arnold, 1930:4 (in checklist of Afrotropical Sphecidae); R. Bohart and Menke, 1976:266 (in checklist of world Sphecidae).

NOMENCLATURAL HISTORY.— The identity of *Tachytes pulchrivestitus* has never been properly understood since its description more than 110 years ago. Turner treated it as a junior synonym of *T. mirus* in 1913 and pointed out to its similarity to *T. rhodesianus* in 1917 (without formally synonymizing these two names). The species was not mentioned by Arnold (1923), but was listed as a synonym of *T. mirus* by Bohart and Menke (1976). My examination of the holotype in 2019 demonstrates that *T. pulchrivestitus* is a valid name and a senior synonym of *T. rhodesianus* Bischoff, 1913 and of *T. midas* Arnold, 1929 (see below), not a synonym of *T. mirus*.

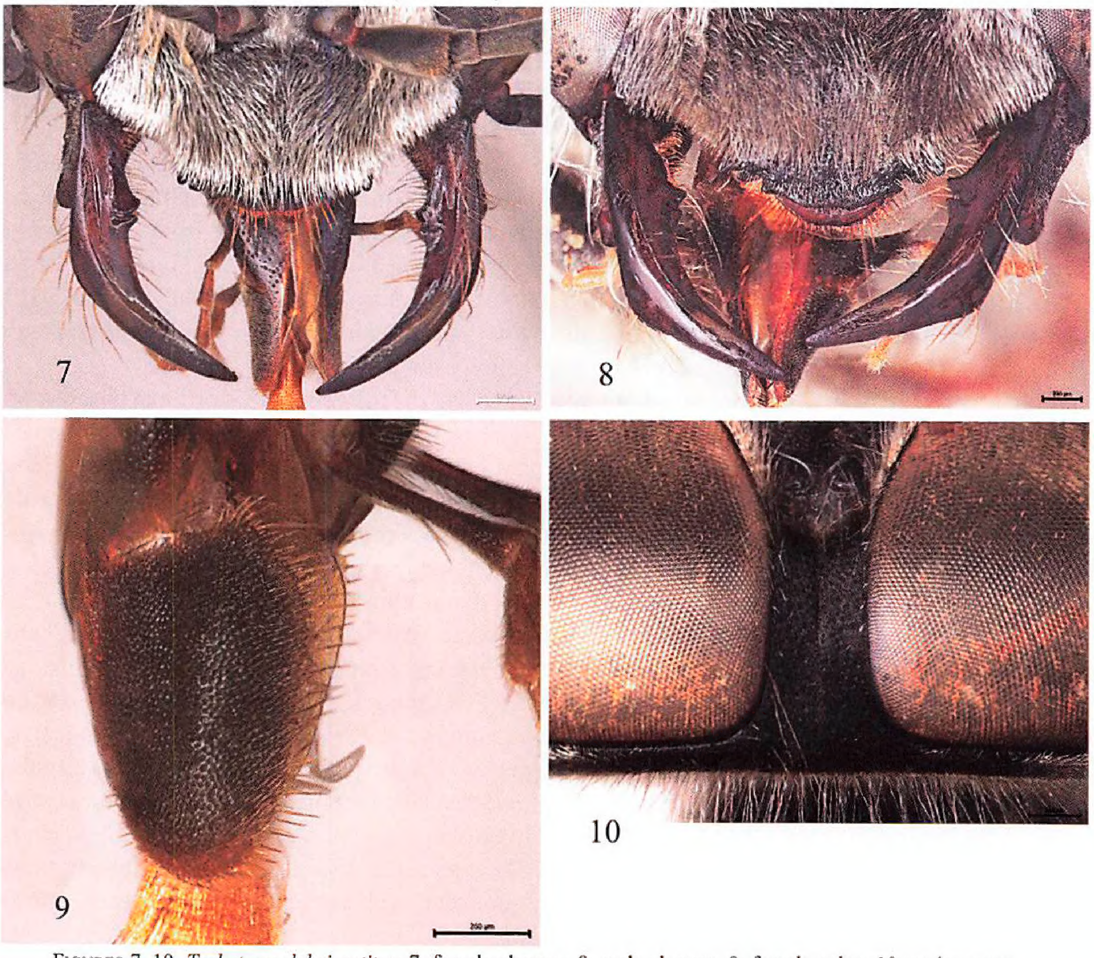
SPECIES STATUS.— Cameron did not mention the length of the galea in his original description of *T. pulchrivestitus* and Turner (1913), when he synonymized this species with *T. mirus* (apparently without seeing its type), must have thought that both species have an equally elongate galea and the first article of the labial palpus. In reality, the galea of *T. pulchrivestitus* is longer that wide (Fig. 9), but shorter than the scape (0.7-0.9 × its length), whereas in *T. mirus* the galea is longer than the scape (about 1.3 × its length). This difference alone precludes the two species from being conspecific. *Tachytes pulchrivestitus*, therefore, is not a synonym of *T. mirus*.

RECOGNITION CHARACTERS.— *Tachytes pulchrivestitus* resembles the species of the *basilicus* species group in having the setae of the gastral terga golden, arranged in a checkered pattern (as in Fig. 1), as well as the palpal formula 6 + 4. Unlike that group, it has the galea longer than wide (Fig. 9) but shorter than the scape (longer than the scape in the *basilicus* group), the basal article of the labial palp less elongate, and the middle clypeal lobe more prominent (Figs. 7 and 8). In the male, the least interocular distance (Fig. 10) is at least equal to the distance between the ventral ends of the hindocelli (rather than smaller), larger in most specimens. Subsidiary recognition characters are: scapal venter and hindfemoral venter with erect setae; hindfemoral apical lobe narrow, insignificant; female sternum II minutely, closely punctate, with larger, sparse punctures, apical depressions setose; antenna, legs, and gaster all black.

A similar species is *T. dilaticornis* Turner, which differs by the absence of erect setae on the scape, by the setae of hindfemoral venter inconspicuously short, almost absent, and in the female by a well-defined, round apical hindfemoral lobe. These features were not observed by Arnold (1923). In the male, the basal flagellomeres are conspicuously expanded ventrally, as described by Turner (1916) and Arnold (1923).

Justification of new synonymy.— Arnold (1929:389) differentiated the syntype female of *T. midas* from the holotype of *T. rhodesianus* by the details of the scutal punctation and the relative length of flagellomeres I and II. In the first species, according to him, the "anterior third of the mesonotum [correctly: scutum] has a microscopic fundamental puncturation over which is scattered a fairly abundant and larger puncturation" and "the second [correctly: first] joint of the flagellum is very slightly longer than the third [correctly: second] joint". In the female of *T. rhodesianus*, the scutum has "a very fine and very close puncturation all over", and flagellomere I is "a little more than one-third longer than the II joint". These subtle differences are individual rather than specific: they break down when more specimens are examined.

Also, the lectotype of *T. midas* and the holotype of *T. pulchrivestitus* each have six rake spines on foretarsomere I, whereas the holotype of *T. rhodesianus* and additional two specimens from Zimbabwe have five. This difference is unimportant, however, as the number of the foretarsal rake spines is known to vary individually in *Tachytes*.



Figures 7–10. *Tachytes pulchrivestitus*: 7: female clypeus; 8: male clypeus; 9: female galea; 10: male vertex.

In the original description of *T. midas*, Arnold (1929:389) claimed that the male genitalia are very different in that species and in *T. rhodesianus*. I could examine the genitalia of a male syntype of *T. midas* as well as of four other specimens. In all of them the gonocoxite shows in the lateral view the dorsal spine shortly after its midlength, as in Arnold's Fig. 12 (for *T. midas*), and in most also the preapical spine in the dorsal view, as in his Fig. 13 (for *T. rhodesianus*). In the specimen from Zambia, however, the dorsal preapical spine is present only on the right gonocoxite whereas the left gonocoxite is smooth. Evidently, the supposed difference in genitalia does not exist.

In conclusion, *T. pulchrivestitus* shares all the diagnostic characters with both *T. rhodesianus* and *T. midas* and is certainly conspecific with them. As it was described earliest, it becomes the valid name for the species.

Geographic Distribution (Fig. 11).— Botswana, South Africa, Tanzania, Zambia, and Zimbabwe. Berland (1942) recorded *T. pulchrivestitus* from Mali (as *T. rhodesianus*), but his identification is not certain.

Records (except the types of *Tachytes midas*, *T. pulchrivestitus*, and *T. rhodesianus*, all other specimens here recorded are from the California Academy of Sciences collections).

Botswana: Serowe (1 ♂).

South Africa: **Limpopo**: 21 mi. S Messina (2 ♂), near Thabazimbi (1 ♂). **KwaZulu-Natal**: Mfongosi (1 ♀, determined as *T. rhodesianus* by G. Arnold), Ntambanana at 28°35′S 31°44′E (1 ♀, determined as *T. rhodesianus* by G. Arnold), 10 mi. N Ubombo (1 ♂). **Mpumalanga**: Songimvelo Nature Reserve at 26°2′33″S 31°00′5″E (2 ♂).

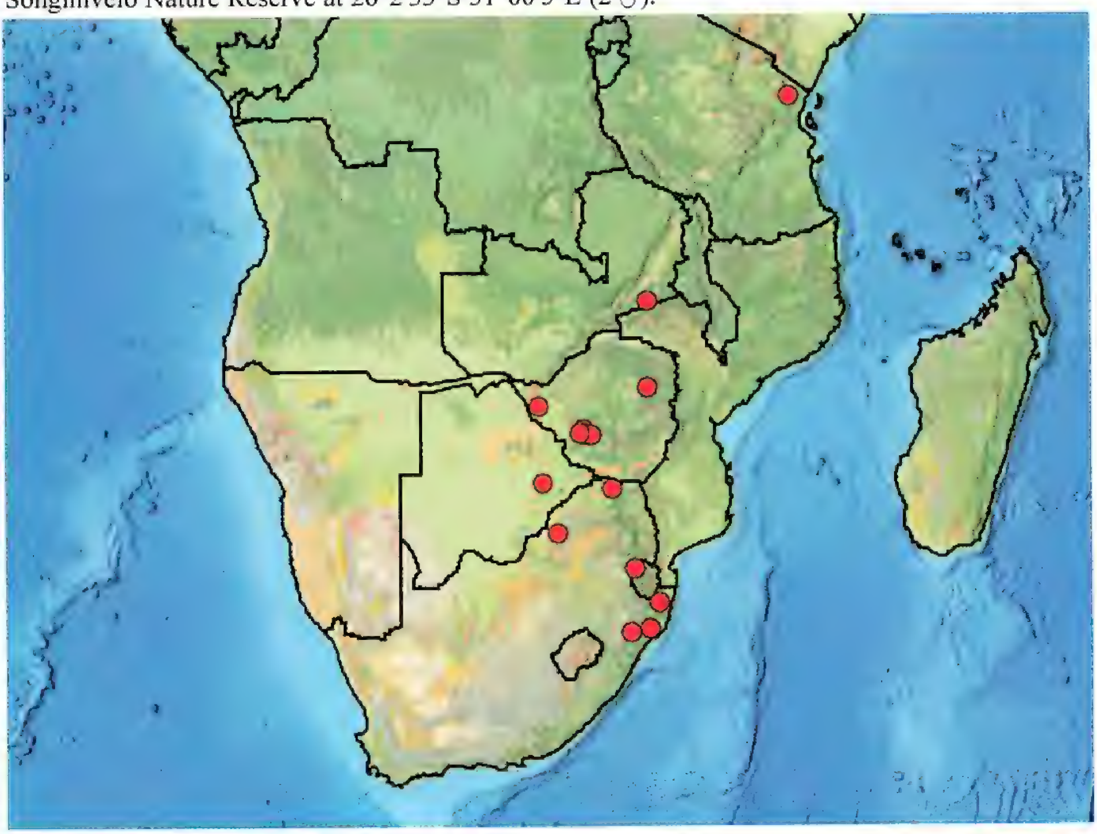


Figure 11. Collecting localities of *Tachytes pulchrivestitus*.

TANZANIA: **Tanga Region**: Mombo (1 ♀, NRS, holotype of *Tachytes pulchrivestitus*).

ZAMBIA: 32 km E Petauke at 14°17′S 31°37′E (1 ♂)

ZIMBABWE: Bulawayo (1 ♀, SAM, lectotype of *Tachytes midas*), Bulawayo airport at 20°00′S 28°38′E (1 ♀), Bulawayo: Hillside (1 ♂, SAM, paralectotype of *Tachytes midas*), Esigodini at 20°17′S 28°56′E (Arnold, 1929, as Essexvale), Hwange National Park (4 ♂, as Wankie), Kami (= Khami) Ruins at 20°09′S 28°26′E (1 ♀, 1 ♂), Springvale (1 ♀, SAM, holotype of *Tachytes rhodesianus*).

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I sincerely thank Simon van Noort and Aisha Mayekiso of the Iziko Museum of South Africa, Cape Town, South Africa, Hege Vårdal of the Naturhistoriska riksmuseet, Stockholm, Sweden, and Viola Richter of the Museum für Naturkunde Berlin, Germany, for sending the types examined in this paper. Robert L. Zuparko (California Academy of Sciences) carefully rewieved the text, suggested several improvements, and eliminated several errors. Erin Prado (Oakland, California) produced color illustrations of morphological characters using the Automontage software package by Syncroscopy. Jere Schweikert (San Rafael, California) generated a locality database that Erika Garcia (Denver, Colorado) used to produce distribution maps, and Michele Esposito (California Academy of Sciences), using Adobe Photoshop®, most thoughtfully helped to improve the color balance of several images.

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A New Species of the New Zealand Endemic Genus *Actenonyx* White, 1846 (Coleoptera: Carabidae: Odacanthini) with Notes on Variation, Distribution, and Habitat

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A second species of the previously monobasic genus *Actenonyx* White, 1846, (Coleoptera: Carabidae: Odacanthini) is described as *A. aotearoa* sp. nov. (type locality: east end of Homer Tunnel, 915 m, Fiordlands National Park, South Island, New Zealand). This species apparently occurs on both North and South Islands, but geographical variation in external morphology and elevational distribution hints that this may actually be a species complex.

KEYWORDS: Adephaga, Carabidae, Odacanthini, *Actenonyx*, new species, New Zealand, endemism

During a visit with my family to South Island, New Zealand, in December, 1993, I was able to realize a long-held dream to sample the unique carabid beetle fauna of that beautiful land. Among materials that I collected, under a permit from the Department of Conservation, Conservation Te Papa Atawhai, and with the assistance of several of my children and local colleagues at various stops, were a number of specimens of genus *Actenonyx* White, 1846. This is a New Zealand endemic genus known from a single species. We collected several series of specimens from both lowland and montane habitats and it seemed to me that specimens from these different elevations differed slightly in their elytral shape and degree of dorsal metallic reflection.

Genus *Actenonyx* was described initially from material collected during the historic 1839-43 voyage of the Erebus and the Terror to the southern end of the World under the command of Captain James Clark Ross. White named the species on which he based his genus *Actenonyx bembidioides*, presumably because of its superficial resemblance to members of genus *Bembidion* Latreille. In fact, he suggested that this new taxon represented a distinct subfamily of Carabidae, but he presented no solid evidence for such status. His description was so general and devoid of distinctive characteristics that the genus was described a second time, by Bates (1867), as genus *Sphallax* with type species *Sphallax peryphoides* Bates. Sometime thereafter, Bates was able to examine a specimen of *A. bembidioides* in the British Museum and concluded that both his genus and species were synonymous with White's respective taxa (Bates 1871, 1874). He agreed with White in suggesting that this taxon represented a distinct subfamily, the Actenonycinae, and noted a unique suite of features of the mouthparts, prothorax, elytra, and legs as evidence. He also suggested that the group might be "near" to the Odacanthinae.

With the exception of Bates' junior synonym of *A. bembidioides*, there have been no additional

species of *Actenonyx* proposed in the last 175 years. However, the genus has remained a taxon of interest over this entire period, particularly with regard to its relationship to other carabid taxa. Broun (1880) included *Actenonyx*, but not *Scopodes*, in his "Group Lebiidae" in "Family Carabides". Csiki (1932) included the genus in his tribe Scopodini along with *Pentagonica* Schmidt-Göbel and *Scopodes* Erichson. Britton (1940) included *Actenonyx* among the lebiines in his key to tribes of New Zealand carabids, as well as in his key to lebiine genera (Britton 1941), but he also suggested that it was actually more closely allied to the odacanthines (Britton 1941:185) than lebiines. Ball et al. (1995) placed *Actenonyx* within the Lebiini based on a phylogenetic analysis of morphological features, particularly of the mouthparts and chaetotaxy of the head; and this placement was followed by Lorenz (2005) and Larochelle and Larivière (2001). However, this analysis did not include any odacanthine taxa. In contrast, results from Liebherr's (2016) phylogenetic analysis of 119 morphological characters for 78 odacanthine taxa with *Celaenephes* Schmidt-Göbel as outgroup placed *Actenonyx* in its own subtribe as sister group to the remaining Odacanthini. A phylogenetic analysis of molecular data by Ober and Maddison (2008) also placed *Actenonyx* as sister to *Scopodes* in a clade with *Pentagonica* and odacanthines. Consequently, the preponderance of evidence supports the placement of *Actenonyx* in a clade with odacanthines rather than with lebiines.

Upon returning home to the California Academy of Sciences, I prepared the specimens collected for study and made dissections of genitalia of both males and females, particularly from each of the localities where we had found *Actenonyx* specimens. From these dissections, it was immediately clear that both male and female genitalia from our montane and lowland samples could be easily distinguished and undoubtedly represented two distinct species. In order to better understand the distributions of the two species and determine which, if either, of the two forms corresponded to *A. bembidioides*, I requested and received the loan of as much material as possible from the British Museum and the U.S. National Museum of Natural History, including the type of *A. bembidioides* from the former institution. I quickly was able to confirm that our lowland material was in every way similar to the *A. bembidioides* type. However, much to my surprise, I found specimens of the new species also represented in the material borrowed from both collections, as well as in the collection at my home institution, and from localities on both North and South Islands. The differences that I had seen in elytral shape and metallic reflection between members of the montane and lowland samples were not as reliably present throughout the ranges of both species on both islands. Complicating what had I thought would be a simple montane/lowland split, specimens with genitalia of the new species from North Island were not clearly associated with montane habitats and a few specimens of *A. bembidioides* from North Island had been collected in montane habitats. Before I could try to resolve this confusing evidence, I had to set this project aside and I have just recently been able to return to it.

The purpose of this report is to describe a new species of *Actenonyx* and to call attention to the morphological and perhaps also ecological variation apparently present in that species.

Materials and Methods

Materials. A total of 229 specimens of *Actenonyx* were examined during this study, including the primary type specimen of *A. bembidioides*. Codens used throughout this report for collections from which specimens were borrowed and/or in which specimens, including primary types, are deposited are as follows:

BMNH	Natural History Museum, London, United Kingdom
CASC	California Academy of Sciences, San Francisco, California, 94952 U.S.A.

CMNZ Canterbury Museum, Christchurch, New Zealand
NMNH United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560 U.S.A
NZAC New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand

Examination of specimens. Specimens were examined using a Leica MZ9.5 stereoscopic microscope or a Wild M5 stereoscopic microscope and a Proline 80 LED Ring Illuminator.

Measurements. The following measurements were recorded for specimens examined: body length (BL), measured from the apex of the longer mandible to the apex of the longer elytron; pronotal length (LP), measured along midline from anterior margin to posterior margin; and pronotal width (WP), measured at the widest point. The ratio of pronotal length to width (LP/WP) was calculated based on those measurements. All measurements were taken with the aid of the Wild M5 stereoscopic microscope fitted with ocular grid and calibrated scale reticles.

Dissection and preparation of male and female genitalia for study. Specimens were relaxed in hot (near boiling) soapy water, then membranes between the genital capsule and tergite VII and sternite VII were severed and the capsule extracted intact. The dissections were then cleared in warm 10% KOH and further dissected to separate the sclerotized parts enough to visualize structures to be compared. Following dissection, preparations of female genitalic structures were stained with Chlorazol Black E®. Terms used for structures of the female genitalia and reproductive tract follow those used by Liebherr & Will (1998) and Liebherr (1990, 2016). I refer to the apical portion of the male median lobe distal to the apical orifice as the apical lamella (Kavanaugh and Liang 2021).

Illustrations. Digital images of whole specimens and particular structures were taken using a Leica imaging system including an M165C dissecting microscope, DFC550 video camera, and two KL1500 LCD light sources. Stacked images were captured and combined into single montage images using the Leica Application Suite V4.2.0. Plates of images were created using Adobe Photoshop CS5.

Distributional data. Locality records reported here include only those for which I examined specimens. No attempt was made to include any other records. Locality records for each species were organized to be consistent with the geographical areas proposed by Crosby et al. (1976, 1998)

SYSTEMATICS

Genus *Actenonyx* White

Actenonyx White, 1846:2. Type species: *Actenonyx bembidioides* White, 1846:2, by monotypy.
Sphallax Bates, 1867:55. Type species: *Sphallax peryphoides* Bates, 1867:56, by monotypy. Generic synonomy recognized by Bates, 1874:275.

Notes on nomenclature and types.— As Bates (1874) stated when he recognized the synonymy of his genus *Sphallax* with *Actenonyx*, "White's description omits all the essential characters of this curious Carabid [sic], and is so vague that there are no means of identifying it without reference to the type." Bates' (1867) description of *Sphallax* was far more informative and useful.

Diagnosis.— Liebherr (2016) suggested the following combination of features as diagnostic of the monogeneric odacanthine subtribe, Actenonycina: antennomeres 2 and 3 glabrous; genae with a ventral seta present; pronotum with disc bearing shallow transverse wrinkles, lateral setae absent; tarsomeres 5 with reduced ventral setation (only three short ventrolateral setae on each side); and median lobe of male aedeagus evenly narrowed apically.

Examination of the material at hand has shown that two of these features are not universally

diagnostic for members of this subtribe and genus. Liebherr recorded antennomeres 2 and 3 as glabrous (his Character 7, state 0). However, in all the specimens I have examined, antennomeres 2 and 3 have at least a few scattered fine setae along their length in addition to the apical whorl of fixed setae (Liebherr's state 1). In some specimens, the density of this pubescence on the apical half of antennomere 3 is nearly one-third of that of the more distal antennomeres. Although most specimens of *Actenonyx* have the lateral pronotal setae absent (Liebherr's Character 36, state 0), some specimens of the new species described below have a single setae present on each lateral margin (Liebherr's Character 36, state 1) at about the basal one-third (see below for further discussion of the occurrence of this feature).

Two other features recorded in the literature appear to be erroneous. Bates (1867) stated that the male protarsi had four tarsomeres "moderately dilated, triangular; clothed beneath with a dense brush of short hairs". Among the specimens I have examined, only protarsomeres 1 to 3 are clearly wider than in females and bear pads of adhesive setae ventrally (no pads seen on protarsomere 4). Larochelle and Larivière (2001) listed *A. bembidioides* as "brachypterous, incapable of flight". However, all of the specimens of both species of *Actenonyx* that I have examined have hindwings that are large, apically folded, and with a reflexed tip and should be able to support flight.

Geographical distribution and diversity.— This genus is a New Zealand endemic. It is widely represented on both North and South Islands, but has not been recorded from Stewart Island or any of the Offshore Islands. It includes just two known species, including the second species newly described here.

Key to Adults of *Actenonyx* Species

1 Protarsi with tarsomeres 1 to 3 distinctly broader and bearing pads of adhesive setae ventrally. . . .male 2

Protarsi with tarsomeres 1 to 3 slender and without pads of adhesive setae ventrally . . . . .female 3

2 Median lobe of male genitalia (Fig. 2A-B) less arcuate in lateral view, apical lamella shorter, more broadly rounded apically, and nearly centered on shaft in dorsal view; last visible abdominal sternite (VI) with two pairs of apicoparamedial setae (one or three setae present unilaterally or bilaterally in a few specimens) . . . . *A. bembidioides* White

Median lobe of male genitalia (Fig. 2C-D) more arcuate in lateral view, apical lamella longer, more narrowly rounded apically, and slightly deflected right of center on shaft in dorsal view; last visible addominal sternite (VI) with only one pair of apicoparamedial setae . . . . ***A. aotearoa* sp. nov.**

3 Ovipositor of female (Fig. 3C) with gonocoxite 2 distinctly longer than gonocoxite 1, tergite IX (Fig. 3A) longer, apical margin projected medially and more convex, sclerotization/pigmentation pattern with middle transverse band and apicoparalateral arms thicker and not sharply defined, apicoparalateral arms not extended laterally along the margin (Fig. 3A); intersegmental membrane ventrad tergite IX (Fig. 3C) with distinctly longer and denser setae (at least medially); elytra, with slight to distinct aeneous metallic reflection in most specimens (without or with faint green or blue metallic reflection in a few specimens), elytral silhouette (Fig. 1A) subrectangular, humeri more narrowly rounded . . . . *A. bembidioides* White

Ovipositor of female (Fig. 3D) with gonocoxite 2 distinctly shorter than gonocoxite 1, tergite IX (Fig. 3B) shorter, apical margin broadly truncate, sclerotization/pigmentation pattern with middle transverse band and apicoparalateral arms more slender and sharply defined, apicopar-

alateral arms extended to apical margin and recurved laterally along the margin (Fig. 3B); intersegmental membrane ventrad tergite IX (Fig. 3D) with distinctly shorter and sparser setae; elytra without or with slight blue metallic reflection, elytral silhouette (Fig. 1B) subvoid, humeri more broadly rounded . . . . ***A. aotearoa* sp. nov.**

***Actenonyx bembidioides* White**

Figures 1A, 2A-B, 3A, 3C, 4, 6

Actenonyx bembidioides White, 1846:2. Lectotype, here designated, a female, in BMNH, labeled: "Type" [printed on white circular label with red ring around text]/ "Colenso" [handwritten]/ "Actenonyx bembidioides White Zool. Erebus & Terror." [handwritten]/ "LECTOTYPE *Actenonyx bembidioides* White,1846 designated by D.H. Kavanaugh 2022" [red label]. Type locality: New Zealand, North Island, Manawatu-Wanganui, Colenso [locality of lectotype].

Sphallax peryphoides Bates, 1867:56. Type series comprised of three syntypes, including both sexes, place of deposition unknown. Specific synonymy recognized by Bates (1874:275).Type locality: New Zealand, Christchurch area.

Notes on nomenclature and types.— Neither White (1846) nor Bates (1867) designated a precise type locality in their original descriptions, although Bates (1874) subsequently listed "Christchurch" as the locality for his type material. It is unclear how many specimens White had at hand when he described *A. bembidioides*, hence the designation of a lectotype. It is also unclear why he did not cite Colenso as the type locality, but I here restrict it to that area because that is the locality for the lectotype.

Despite the efforts of curators in both BMNH and CMNZ, Bates' type series of *A. peryphoides* has not yet been located. If and when it is found, a lectotype should be designated. Even without reference to the type series, Bates' description of that nominal taxon, with a reference to the "obscure bronze colour" of the dorsum, is sufficient to assure me that his type series represented what I am identifying here as *A. bembidioides* and not the new species described below (see Diagnosis below).

Diagnosis.— Dorsal surface of elytra without or with faint to distinct aeneous metallic reflection; tooth of mentum slightly to moderately emarginate (bifid) medially; elytral silhouette subrectangular (Fig. 1A), humeri narrowly rounded, base broad, basal margin nearly straight laterally, subangulate or slightly sinuate paramedially, discal pore punctures only slightly foveate; abdominal sternite VI in most males with two pairs of apicoparamedial setae (one or three setae present unilaterally or bilaterally in a few specimens), in females with two pairs; median lobe of male genitalia (Fig. 2A-B) straighter, less arcuate, in lateral aspect, apical lamella short, broadly rounded apically and nearly centered on shaft in dorsal aspect; female genitalia with tergite IX longer (Fig. 3A), with apical margin slightly projected medially and narrowly convex and with sclerotization/pigmentation pattern with middle transverse band and apicoparalateral arms thicker and not sharply defined, apicoparalateral arms not extended laterally along the margin (Fig.3A), intersegmental membrane ventrad tergite IX with long and dense setae, ovipositor (Fig. 3C) with gonocoxite 2 (="gonocoxite" of Deuve (1993)) distinctly longer than gonocoxite 1 (="gonosubcoxite" of Deuve (1993)).

Comments.— The most reliable features for distinguishing members of this species from those of the new species described below involve the male and female genitalia. Genitalic features of both sexes differ markedly between the two species. Unfortunately, while each of the external features listed in the key and/or in the diagnosis above distinguish most members of these two species, none of them clearly distinguish all specimens. Examination of genitalic features is recommended to confirm identifications for either sex.

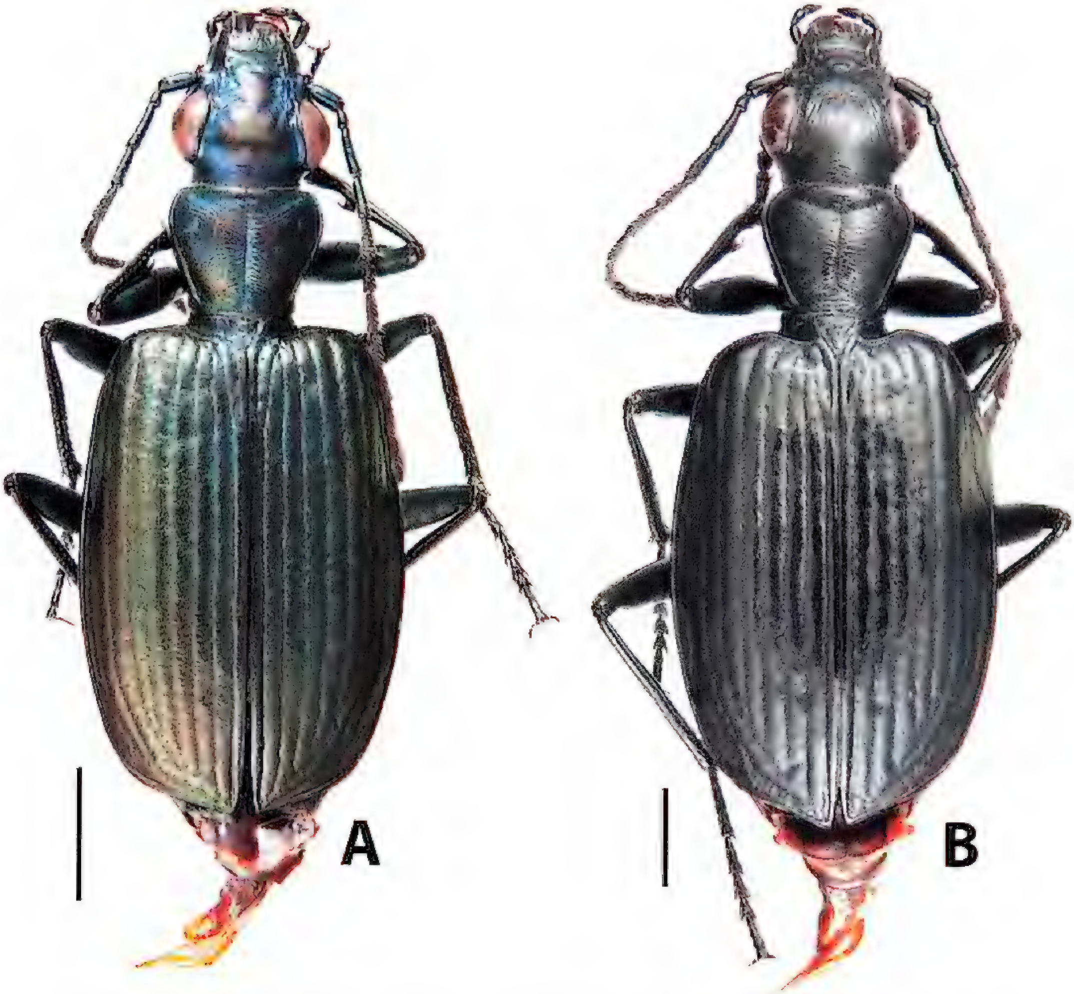

FIGURE 1. Dorsal habitus of *Actenonyx* species. A. *A. bembidioides* White (South Island, Southland, Te Anau Downs, Mistletoe Creek, 216 m); B. *A. aotearoa* sp. nov. (South Island, Fiordlands National Park, east end of Homer Tunnel, 915m). Scale lines = 1.0 mm.

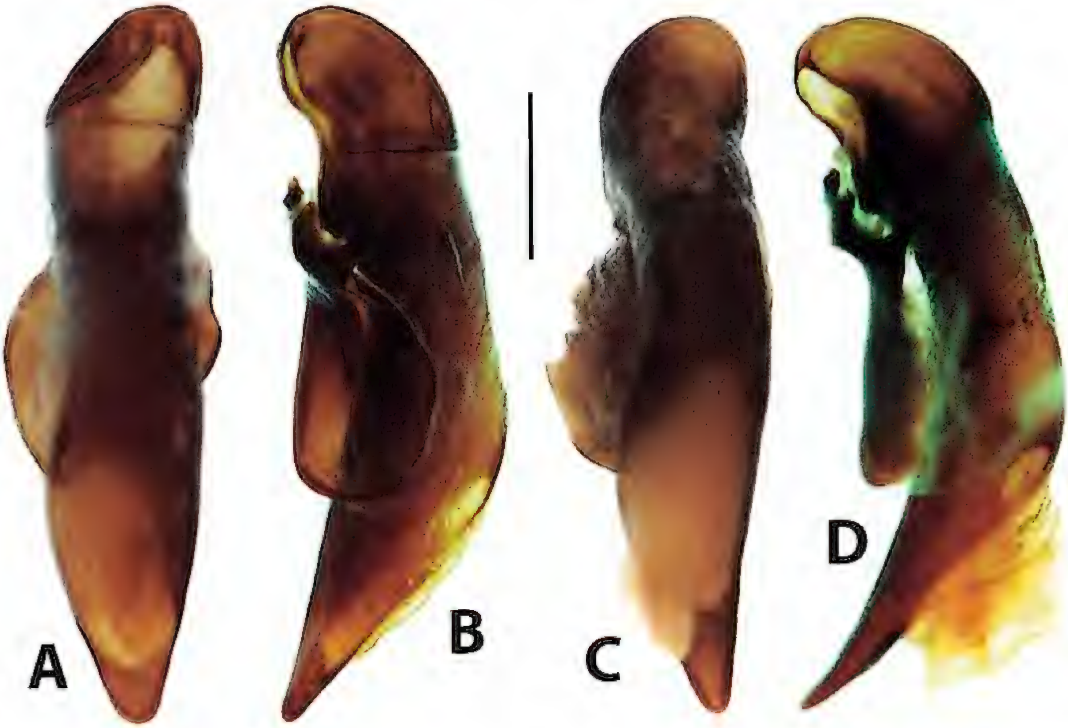

FIGURE 2. Male genitalia of Actenonyx species. A and B. *A. bembidioides* White (South Island, Southland, Te Anau Downs, Mistletoe Creek, 216 m); C and D. *A. aotearoa* sp. nov. (South Island, Fiordlands National Park, east end of Homer Tunnel, 915m). A and C. Dorsal aspect; B and D. Left lateral aspect. Scale line = 0.5 mm.

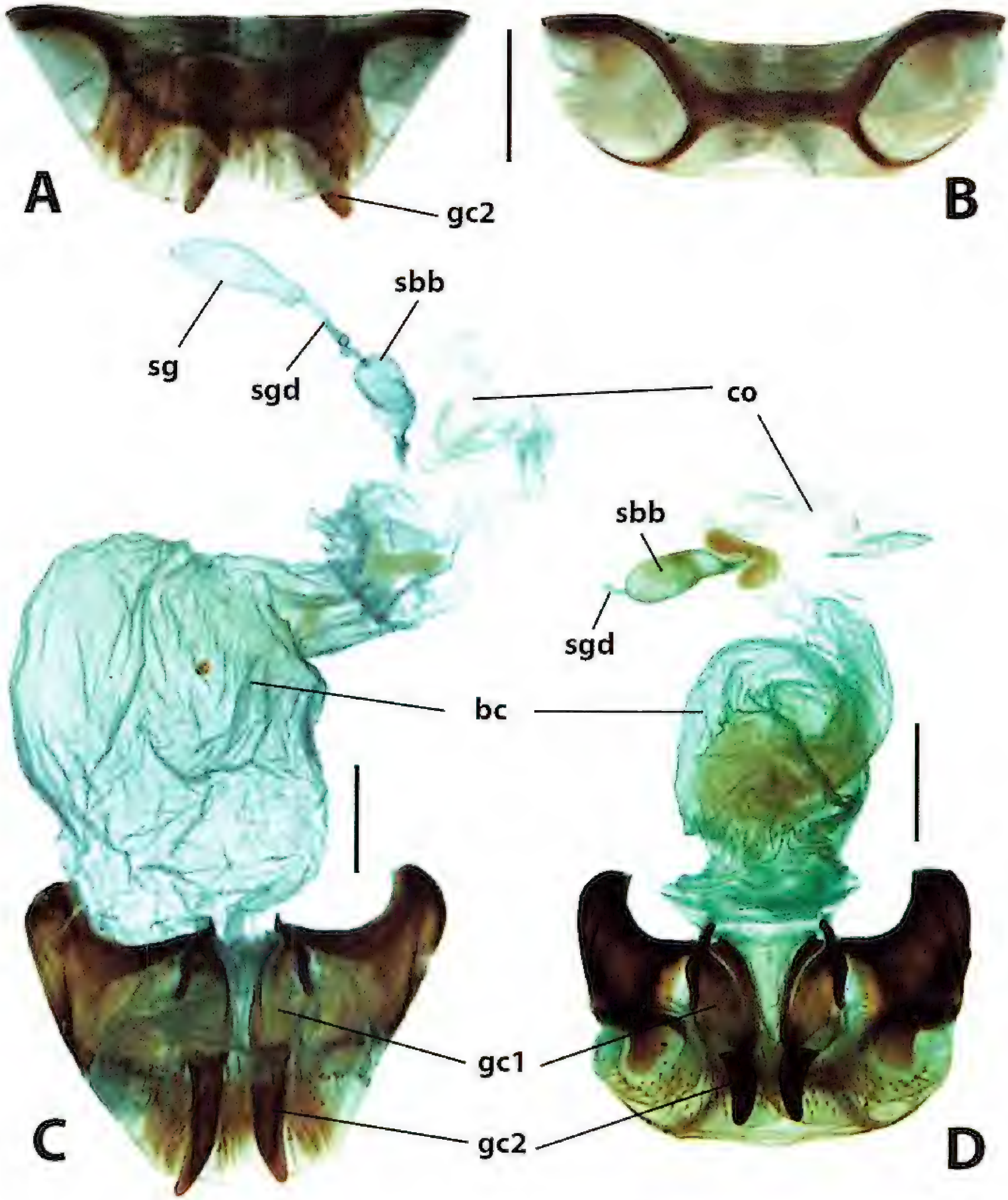

FIGURE 3. Female genitalia and reproductive tract. A and C. *A. bembidioides* White (South Island, Southland, Te Anau Downs, Mistletoe Creek, 216 m); B and D. *A. aotearoa* sp. nov. (South Island, Fiordlands National Park, east end of Homer Tunnel, 915m); A and B. Tergite IX, dorsal aspect; C and D. Genital capsule and reproductive tract; bc = bursa copulatrix; co = common oviduct; gc1 = gonocoxite 1; gc2 = gonocoxite 2; sbb = spermathecal basal bulb; sg = spermathecal gland; sgd =spermathecal gland duct. Scale lines = 0.5 mm.

Geographical distribution.— This species is widely distributed throughout North and South Islands of New Zealand but has not been recorded from Stewart Island or any of the Offshore Islands (Larochelle and Larivière 2001). I examined a total of 159 specimens (84 males and 75 females) from the following localities (Fig. 4): North Island. Auckland: Auckland (Broun collector; one female, BMNH). Bay of Plenty: White Pine Bush (14 March 1967, T.H. Davies collector; one male and two females, NMNH). Coromandel: Tairua (two males, BMNH). Northland: Mangamuka River (at Hokianga Harbour, 9 January 1924, A. Richardson collector; one female, BMNH). Rangitikei: Colenso (one female, BMNH). Taranaki: Mount Egmont (1520 m; one female, BMNH). Taupo: Erua (28 December 1940, C.E. Clarke collector; three males and one female, BMNH); Mount Ruapehu (980 m, 12 February 1938; three males and one female, BMNH); Ohakune (1 October 1919, T.R. Harris collector; one male, BMNH), (December 1922, T.R. Harris collector; two males, BMNH), (December 1922, T. R. Harris collector). Wanganui: Rangitikei River (near Porewa, March 1941, S. Gibbs collector; four males, BMNH); Wairua (one male, BMNH). Wellington: Lower Hutt (February 1976; five males and one female, NMNH). Waikato: Waipa River (at Otewa Gorge, 23 February 1941; one male, BMNH). South Island. Buller: Greymouth (Maori Creek; one female, BMNH), (Helms; three males and six females, BMNH), (3 November 1880, Helms collector; one male, BMNH), (1885, Helms collector; one female, BMNH). Dunedin: Mount Maungatua (610 m, 9 December 1923; one female, BMNH). Fiordland: Lake Manapouri (Hope Arm, 6 January 1929; one male and one female, BMNH); Lake Te Anau (Mistletoe Creek at Te Anau Downs, 216 m, 22-23 December 1993, D.H. and T.W. Kavanaugh collectors; 37 males and 27 females, CASC, BMNH, NZAC); Pompolona (6 November 1986, J.G. Edwards collector; one female, CASC); Te Anau (10 November 1986, J.G. Edwards collector; one female, CASC). Mid Canterbury: Broken River (at Arthur's Pass Road, 30 October 1986, J.G. Edwards collector; one male, CASC); Cass (27 December 1942, A. Richardson collector; one male, BMNH). North Canterbury: Hurunui (one male, BMNH). Nelson: Cobb River (23 November 1977, E. I. Schlinger collector; one female, CASC); Mount Arthur (Brookes collector; one female, NMNH); Wangapeka (one male, BMNH); Wangapeka Valley (18 November 1934, E.S. Gourlay collector; one female, CASC); Westport (November-December 1901, J.J. Walker collector; one male, BMNH). Otago Lakes: Arrow River (at Arrowtown, 22 December 1993, D.H. Kavanaugh collector; two males and three females, CASC); Route Burn River (6 January 1945, C.E. Clarke collector; one female, BMNH); Young River (20 km above Lake Wanaka, 10 December 1994, W.W. Middlekauf collector; one female, CASC), (20 km above Lake Wanaka, 29 November 1992, W.W. Middlekauf collector; one male and one female, CASC). South Canterbury: Lake Tekapo (one male, BMNH). Southland: Wyndham (6-10 March 1982, W.W. Middlekauff collector; one male, CASC). Locality unknown. (one male, NMNH); (A. Swak collector; one male and one female, BMNH); (C. Darwin collector; one female, BMNH); (Koebele collector; one male and two females, CASC); (five males and eight females, BMNH); (three males and six females, NMNH).

Habitat distribution.— Larochelle and Larivière (2001) described a very broad altitudinal range for this species (from lowland to alpine areas) and diurnal activity of both adults and larvae "in sunshine" on "open dry gravelly-stony banks of streams…at some distance from water." In our limited encounters with this species in 1993, my helpers and I found specimens only at low (210 m) to moderate (400 m) elevations on the open banks of small to moderate-size streams (Fig. 6). Beetles were found under stones or in gravel in daytime on a cloudy day and actively running on the surface at night in these same areas, ranging from about 10 cm to 15 m back from the water's edge. The altitudinal range mentioned by Larochelle and Larivière no doubt includes records for the new species, *A. aotearoa*, described below, so the true altitudinal range of *A. bembidioides*

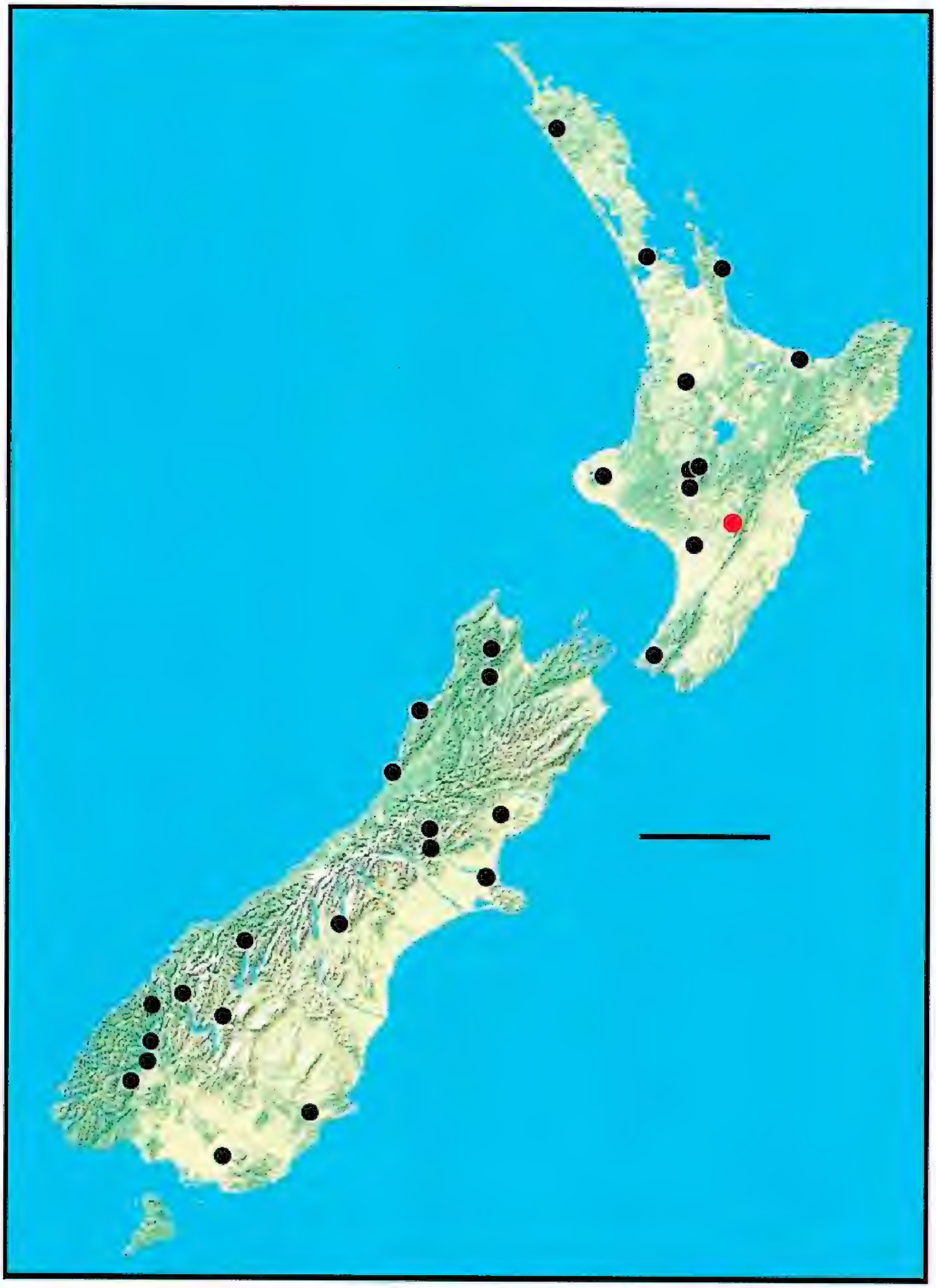

FIGURE 4. Map showing distribution records for specimens of *Actenonyx bembidioides* White examined for this study (red circle = type locality; black circles = other localities). Scale line = 200 km.

alone may be somewhat more restricted than previously considered. It seems likely, however, that the altitudinal ranges overlap at least partially, based on the record of *A. bembidioides* from Lake Tekapo (minimum elevation of 715 m).

Geographical relationships with related species.— The geographical range of this species overlaps broadly with that of *A. aotearoa*, the new species described below. I have examined a few specimens of both species collected on both North and South Islands and labeled as from the same locality, but this does not mean that members of the two species actually were found together (syntopic). Shared records from North Island include Okahune (but specimens collected were in different years), Rangitkei River near Porewa (specimens of both species were collected in March, 1941), and Tairua (no shared dates of collection). Shared records from South Island include Cass (but with different dates of collection and collectors), Lake Tekapo (no dates of collection or collectors named), Te Anau (with different dates of collection and collectors), and Westport (same collector but over a two-month period in 1901). It is certainly possible that the two species are syntopic in some parts of their geographical ranges, but data that I have examined cannot confirm this.

***Actenonyx aotearoa* Kavanaugh sp. nov.**

Figures 1 B, 2 C–D, 3 B,D, 5, 7

Type material.— Holotype, a male, deposited in NZAC, labeled: "NEW ZEALAND, South Island, Fiordlands National Park, east end of Homer Tunnel, 23 December 1993, Stop#93-22A, D.H. & T.W. Kavanaugh col."/ "D. H. Kavanaugh Collection" [orange label]/ "HOLOTYPE *Actenonyx aotearoa* Kavanaugh sp. nov. designated 2022" [red label]. Paratypes (a total of 22): same data as holotype (14 males and eight females; BMNH, CASC, NZAC). All paratypes also bear the following label: "PARATYPE *Actenonyx aotearoa* Kavanaugh sp. nov. designated 2022" [yellow label].

Notes on nomenclature and types.— Variation among some of the specimens that I identify here as members of this new species suggests there may be more than one species represented (see discussion of variation below). Consequently, I am restricting the type series to only those specimens from the type locality. Additional sampling and subsequent study is needed to establish whether my concept of *A. aotearoa* represents a single species or includes two or more species. I have applied standard determination labels to all the non-type specimens to reflect my present identifications.

Type locality.— New Zealand, South Island, Fiordlands National Park, east end of Homer Tunnel, 44.76535°S/167.98949°E, 915 m.

Derivation of species name.— The species epithet is the Maori name for New Zealand, *Aoteoroa*, which means "the land of the long white cloud," a reference to the snow-covered crest of the Southern Alps as first seen from a distance at sea. It is used as a noun in apposition.

Diagnosis.— Dorsal surface of elytra without or with faint blue or blue-green metallic reflection; tooth of mentum truncate or only faintly emarginate medially; elytral silhouette subovoid (Fig. 1B), humeri broadly rounded, base narrowed, basal margin distinctly sinuate paramedially, discal pore punctures more distinctly foveate; abdominal sternite VI in males with one pair of apicoparamedial setae, in females with two pairs; median lobe of male genitalia (Fig. 2C-D) distinctly arcuate, in lateral aspect, apical lamella longer, pointed, narrowly rounded apically, and distinctly deflected right in dorsal aspect; female genitalia with tergite IX (Fig. 3B) short, broadly truncate, only slightly convex apically and with sclerotization/pigmentation pattern with middle transverse band and apicoparalateral arms more slender and sharply defined, apicoparalateral arms extended to apical margin and distinctly recurved laterally along the margin (Fig. 3B), interseg-

mental membrane ventrad tergite IX with short and sparse setae, ovipositor (Fig. 3D) with gonocoxite 2 distinctly shorter than gonocoxite 1.

Comments.— As noted above in the Comments section for *A. bembidioides*, virtually all of the external features noted to distinguish most members of these two species cannot distinguish all members, whether applied singly or even in combination. This confusing overlap in external morphological features is likely the main reason why the existence of at least two separate species has not been recognized previously. Because males and female of the two species recognized here are each easily distinguished on the basis of their genitalic morphology, dissection and examination of these features are recommended to confirm identifications for either sex.The description that follows includes features characteristic of specimens of the type series. Variation in these features beyond what is seen in the type series but found among specimens identified as *A. aotearoa* from other areas is discussed in the section on Geographical variation below.

Description.— ***Size*** small, BL males = 7.5 to 8.0 mm, females = 7.6 to 8.3 mm. Body and all appendages black. Dorsum dull to slightly shiny, without or with slight metallic blue or blue-green metallic reflection. Microsculpture on head comprised of faintly (medially on frons and vertex) to moderately (on occuput) impressed isodiameteric sculpticells, slightly stretched in wrinkled areas; pronotal microsculpture comprised of faintly impressed isodiametric sculpticells, difficult to discern in wrinkled areas; elytral microsculpture comprised of moderately impressed and regular or slightly irregular isodiametric sculpticells.

Head. Labrum truncate or slightly emarginate apically, with two or three pairs of apical setae and sparse and scattered short pubescence. Clypeus with one pair of fixed setae and very sparse and short pubescence laterally. Mandibles moderately elongate, about 1.75 times as long distance between antennal base and apical margin of labrum. Maxilla with galea comprised of two subequal galomeres and free from the lacinia; apical maxillary palpomere glabrous. Antennae with scape moderately long, slightly more than twice as long as wide, cylindrical; antennomeres 2 and 3 with much reduced pubescence compared with that of more distal antennomeres, but with at least a few sparse and scattered fine setae over their length in addition to the apical whorl of fixed setae; all antennomeres concolorous. Frons convex medially with shallow longitudinal wrinkles and very sparse and short pubescence laterally, frontal furrows poorly defined, shallow, and short. Vertex convex and smooth medially, with obliguely-longitudinal wrinkles laterally, with two or three pairs of supraorbital setae present. Eyes large, convex but only moderately projected. Tempora short, oblique. Ventral surface of each gena with a single fixed seta plus a few sparse and very short setae. Mentum: with median tooth present, truncate or slightly emarginate apically (very slightly bifid in a few specimens); suture between mentum and submentum (gula) straight and complete. Submentum with a single seta on each side.

Prothorax. Pronotum subcordate, ratio PL/PW 0.85-0.92, greatest width near anterior one-fourth, narrowest at base; anterior margin straight or slightly concave; lateral margins rounded in anterior one-third, straight in basal two-thirds or slightly sinuate subapically in some specimens; basal margin straight; anterior angles rounded, not at all projected anteriorly; posterior angles rectangular or very slightly obtuse, not at all projected posteriorly; anterior margin without margination; lateral explanation (medial to lateral bead) absent; lateral bead (margination) thin, slightly elevated, extended from anterior angle posteriorly to near posterior angle then roundly continuous with lateral parts of basal margination; basal margination evident laterally but absent or obscured (by transverse wrinkles) medially; pronotal disc with shallow transverse wrinkles throughout and nearly to base, sparsely and faintly punctate peripherally, without parasagittal impressions; anterior and posterior transverse impressions moderately deep, distinct and broad, medial longitudinal impression well-defined, narrow, extended between anterior and posterior

impressions only; midlateral setae absent (but see Geographical variation section below), basolateral setae absent. Proepisterna narrowly visible in dorsal view in basal two-thirds, smooth and impunctate.

Pterothorax. Elytral silhouette subovoid (Fig. 2B), humeri broadly rounded, base narrowed; basal margin distinctly sinuate paramedially, of uniform depth throughout; lateral explanation narrow throughout; posthumeral sinuation of lateral margin shallow but distinct in most specimens, absent from a few, subapical sinuation obsolete, elytral apices obliquely truncate; elytral topography (in cross-section) flat medially and rounded laterally; intervals slightly convex, all almost equally so; striae moderately and broadly impressed throughout, not or only faintly punctulate; parascutellar seta present on each elytron, inserted at base of stria 1, its pore socket not elevated above interval 1; discal setiferous pore punctures slightly to moderately foveate, interval 3 with three to four discal setae (two in a few specimens), the anteriormost inserted in or near stria 3 and the others in or near stria 2; interval 5 with one to seven discal setae inserted in or near interval 4; interval 7 with three to seven discal setae inserted in or near stria 6; umbilicate series comprised of ten to 13 setae arranged in three groups (four or five anterior setae, one middle seta, and five to seven posterior setae); two apical setae present (one near the apex of stria 2 and one near the apex of interval 2. Hindwings present, apparently full-sized (with a folded apex) and functional. Metepisterna about twice as long as wide.

Legs. Metacoxae bisetose, with one seta medially and one laterally at the medial end of the lateral coxal wing. Protarsomeres 1 to 3 of males distinctly broader and more robust than in females and with pads of adhesive setae ventrally, these pads absent from females, protarsomere 4 very slightly more robust in males than in females but without a pad of setae in both sexes; metatarsomeres 4 with short lateral lobes; metatarsomeres 5 with 2 rows of three lateral setae.

Abdomen. Visible sternite II with a small cluster of setae medially between the metacoxae; sternites 3 to 5 with two to seven or more pairs of paramedial setae in rows at midlength of each sternite; sternite VI apically truncate or very slightly convex, in males with one pair of apicoparamedial setae, in females with two pairs; abdominal venter with a few scattered, short, and pubescence-like setae, especially laterally and most abundant on sternite VI. Abdominal tergite VIII of both sexes narrowly divided by membranous cuticle medially into laterotergites.

Male genitalia. Laterotergites VIII with basal apodeme narrow and sclerotized margin incorporating spiracle laterally; mediotergite IX ("ring sclerite") angulate anteriorly, wishbone-shaped. Median lobe distinctly arcuate, slightly narrowed basally, broadest near mid-length and then evenly tapered toward apex in lateral aspect (Fig. 2D); apical lamella long, pointed, narrowly rounded apically, and distinctly deflected right in dorsal aspect (Fig. 2C).

Female genitalia. Tergite IX (= mediotergite IX of Deuve (1993)) (Fig. 3B) broadly truncate, only slightly convex apically, sclerotization/pigmentation pattern with middle transverse band and apicoparalateral arms more slender and sharply defined, apicoparalateral arms extended to apical margin and recurved laterally along the margin (Fig. 3B). Intersegmental membrane ventrad tergite IX with short and sparse setae. Gonocoxite 1 of ovipositor (Fig. 3D) with a fringe of four to seven apicoventral setiform setae and with basal apodeme as in Fig. 3D. Gonocoxite 2, shorter than gonocoxite 1, falciform, acuminate and narrowly rounded apically, with two lateral ensiform setae and one dorsal ensiform seta. Bursa copulatrix (Fig. 3D) membranous, asymmetrically vase-like, with narrower extension to common oviduct and spermathecal assembly, without evident spicules; common oviduct short, attached to bursa proximal to spermathecal assembly; spermathecal assembly with basal bulb narrowly joined by a duct to spermathecal sclerite, spermathecal gland reservoir inserted apically on basal bulb and elongate-ovoid.

Geographical variation.— The size range among all specimens that I have identified as

A. aotearoa is slightly broader (BL males = 6.8 to 8.0 mm, females = 6.5 to 8.8 mm) than that of the type series (BL males = 7.5 to 8.0 mm, females = 7.6 to 8.3 mm). Both the smallest and the largest specimens examined were collected on North Island, with the largest specimens from the Tairua area and the smallest specimens from the Ohakune, Wainuiomata, and Wellington areas. Most surprising was the discovery of specimens with a lateral seta present on each side at or near the apical one-third of the pronotum, inserted partly in the narrow groove just inside the lateral bead and partly on the lateral bead itself. The absence of such setae has been considered a characteristic feature of *Actenonxy* members; and I have not seen any specimen of *A. bembidioides* with these setae present nor are they present in any specimen of type series of *A. aotearoa*. In material that I examined, the occurrence of specimens with these pronotal setae was restricted to localities in the southern part of North Island and one locality on the northern end of South Island (see Fig.5). Although sample sizes were small, all specimens examined from these localities had these setae, and no specimens outside of these areas on either island had them. The presence of the lateral pronotal setal also appears to be correlated with smaller size, at least in the material that I examined. However, as far as I could determine, males and females of all sizes and with or without the pronotal setae share similar genitalia, respectively. Consequently, I have found no basis upon which to recognize more than a single new species, *A. aotearoa*, at this time. Additional distinguishing features may become apparent with stategic sampling and additional material, particularly from North Island and the northern part of South Island.

Geographical distribution.— This species is apparently widely distributed in mountainous parts of both North and South Islands. I examined a total of 72 specimens (36 males and 34 females), including the type series, from the following localities (Fig. 5): NORTH ISLAND. **Coromandel**: Tairua (May 1876; two females, BMNH). **Taupo**: Ohakune (1 October 1919, T.R. Harris collector; one male, BMNH), (December 1922, T.R. Harris collector; two males, BMNH), (December, 1919, T.R. Harris collector; one male, NMNH). **Wanganui**: Rangitikei River (near Porewa, March 1941, S. Gibbs collector; one female, BMNH). **Wellington**: Wainuiomata (16 October 1919 H.V. Hudson collector; one male and one female, BMNH); Wellington (Hudson collector; one female, BMNH), (1891, Hudson collector; three males and three females, BMNH), (one male, BMNH). SOUTH ISLAND. **Buller**: Boatman's Creek (near Reefton; one female, BMNH); Kumara (1884, Helms collector; one male, BMNH); Lake Guyon (two males, BMNH). **Fiordland**: Fiordland National Park, Cleddau River (at Milford Sound, 9 December 1995, W.W. Middlekauff collector; one male CASC), Homer Tunnel (east end, 915 m, 23 December 1993, D.H. and T.W. Kavanaugh collectors; 15 males and eight females, BMNH, CASC, NZAC); Te Anau (19 November 1991, G. Mathieson collector; one female, CASC). **Marlborough**: Hanmer Springs (13 November 1986, J.G. Edwards collector: one female, CASC). **Mid Canterbury**: Arthur's Pass (910 m, 4 January. 1923, Myer collector; one female, BMNH), (3 January 1943, C. E. Clarke collector; one male, BMNH), (1 January 1943, C. E. Clarke collector; one female, BMNH), (1 January 1943, E.S. Gourlay collector; one female, CASC); Arthur's Pass National Park (Klondyke Corner, 645m, 27 December 1993, D.H. Kavanaugh collector; one male, CASC); Bealey (620 m, 27 December 1993, D.H. Kavanaugh collector; one male, CASC); Cass area (910 m, 7 September 1972, C.W. Sabrosky; one female, NMNH); Mount Hutt (December 1911; one male, BMNH). **Nelson**: Abel Tasman National Park (Marahau, 26 January 1995, H. Fischer collector; one female, RSCC); Westport (November-December 1901, J.J. Walker collector; one male and one female, BMNH). **Otago Lakes**: Lake Wanaka (5 January 1949, B. Davidson collector; one male, BMNH). **South Canterbury**: Lake Tekapo (one female, BMNH). **Westland**: Otira (20 February 1919, J.W.Campbell collector; two females, NMNH); Otira River (at Pegler Creek, 3 January 1943, C.E. Clarke; one male, BMNH). LOCALITY UNKNOWN. (G.V. Hudson collector; one male and one

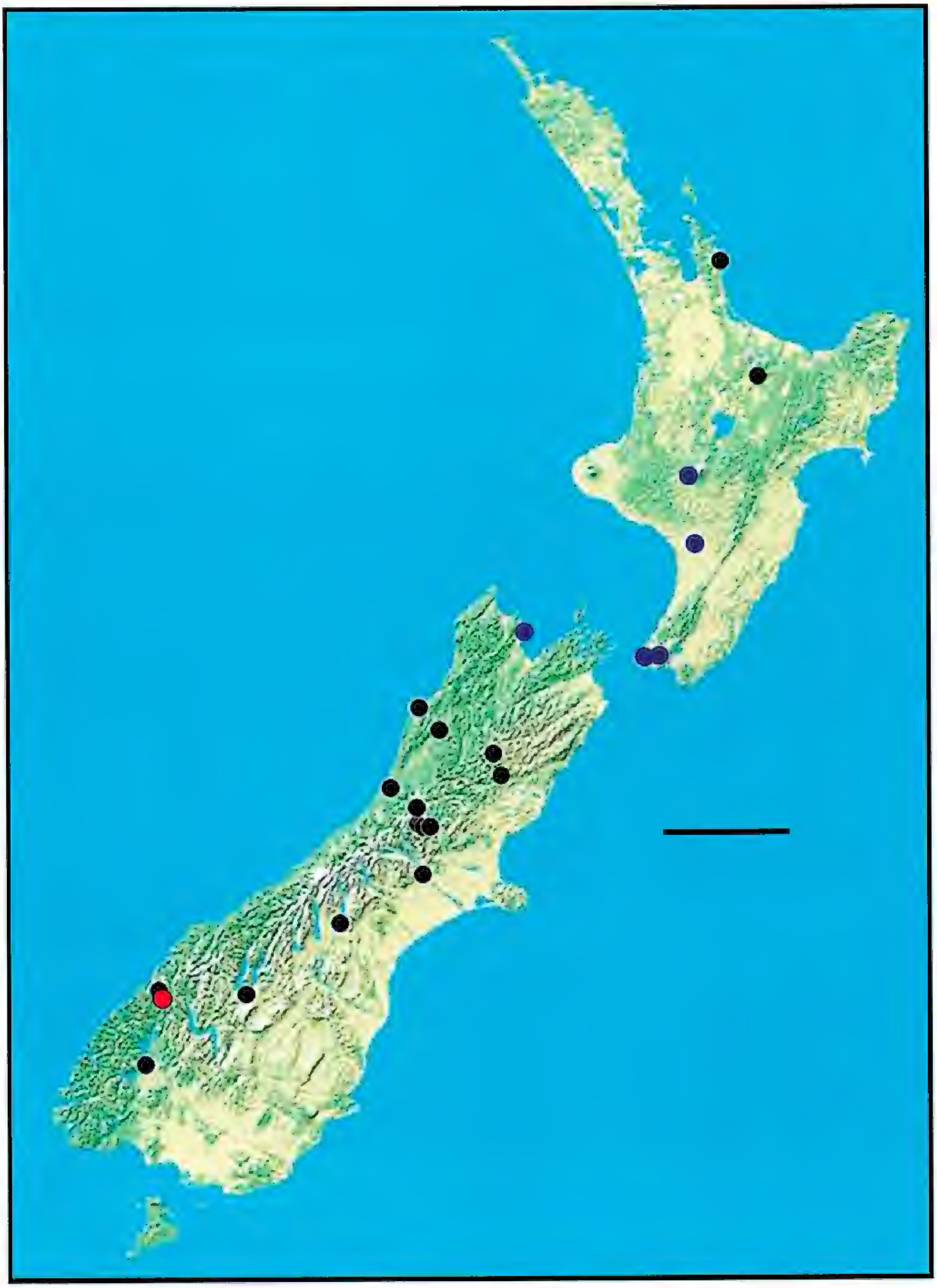

FIGURE 5. Map showing distribution records for specimens of *Actenonyx aotearoa* sp. nov. examined for this study (red circle = type locality; blue circles = localities where specimens have pronotal lateral setae; black circles = other localities). Scale line = 200 km.

female, BMNH); (J.J. Walker collector; two females, BMHN); (Suter collector; two males, BMNH); (one males and three females, BMNH); (C.M. Wakefield collector; one male and one female, BMNH); (T. Broun collector; one female, BMNH); (one female, NMNH).

Habitat distribution.— Specimens of the type series were all collected under stones at the edges of a small snowmelt stream (Fig. 7B) above treeline at an elevation of 915 m. This area was at the base of the east-facing slope of a U-shaped (previously glaciated) valley (Fig. 7A) running north-south on the eastern flank of the Southern Alps. Two additional specimens were collected in the Arthur's Pass area, one under a stone on a broad, flat, braided river bank at Klondyke Corner (elev. 645 m) and the other under a loose stone in a concrete drainage ditch at Bealey (620 m). All of the other locality records listed above were without associated elevational and/or habitat data, so both the elevational and habitat ranges of this species are still only poorly known and require additional study.

Geographical relationships with related species.— The geographical range of *A. aotearoa* as described here overlaps broadly with that of *A. bembidoides* in mountainous parts of both North and South Islands. See this section in the treatment of the latter species above for details.

FIGURE 6. Photograph of habitat for *Actenonyx bembidioides* White. Arrow River at Arrowtown, Otago, South Island.

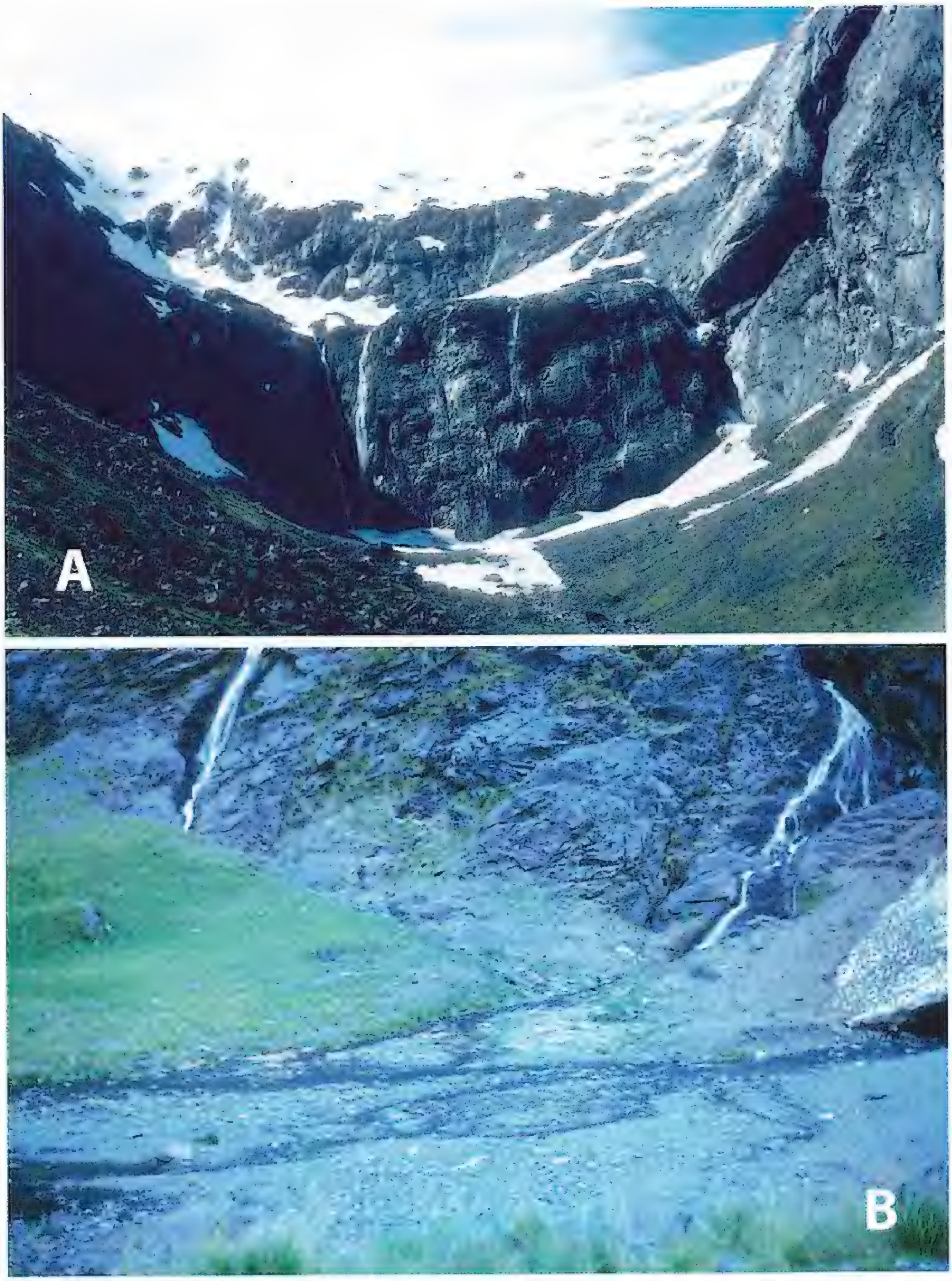

FIGURE 7. Photographs of habitat for *Actenonyx aotearoa* sp. nov. A. Glaciated valley at east end of Homer Tunnel, Fiordlands National Park, South Island, view looking north; B. Snowmelt streams at east end of Homer Tunnel, just south of tunnel entrance.

Discussion

The pattern of geographical variation and distribution seen within the admittedly meager sample of *A. aetearoa* examined here casts some doubt on the conspecificity of all specimens identified as that species, particularly those from North Island and perhaps the northern part of South Island. All specimens from North Island with date or even year of collection recorded were collected more than 70 years ago and none were from areas above 250 m, hence at a lower elevation than any precise records of the species from South Island. For a single species, one would expect any differences in elevational range between North and South Islands to be opposite the observed pattern (i.e, populations on North Island should occupy higher elevations, not lower, than those on South Island). Might this be indicative of differences in habitat preference or physiological adaptation between members of populations on the two islands? The occurrence of some beetles with smaller size and lateral setae present on the pronotum in a region interposed between regions with larger beetles lacking these setae is also intriguing and warrants further study. Phylogeographic studies using molecular data should prove useful for better understand of genetic relationships among populations of *A. aotearoa* both within and between islands and help to determine whether or not this is actually a species complex. Fortunately, these beetles are often abundant and easy to collect where they occur and so should be an ideal group for phylogeographic study. I strongly encourage local carabid enthusiasts in New Zealand to sample widely, preserve material suitably for both morphological and molecular analysis, and keep the detailed records of location, elevation, and habitat needed for a better understanding of these elegant beetles.

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Distinguishing *Scaphinotus mannii* Wickham (Coleoptera: Carabidae: Cychrini), a Species of Conservation Concern, from Similar Congeneric Species

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Scaphinotus mannii **Wickham (Coleoptera: Carabidae: Cychrini) has been known previously from only three sites in southeastern Washington, three recently detected sites in southwestern Idaho, and one site in northeasternmost Oregon. The limited known range and apparent restriction to riparian gallery forests have caused this species to be regarded as potentially threatened or endangered. Recent surveys have yielded many more specimens over a greater area than previously known. Some of these specimens exhibited hitherto unrecognized morphological variation, rendering existing keys unreliable for identification of this species. This paper presents additional characters for distinguishing *S. mannii* from the two other species of *Scaphinotus* (*Pseudonomaretus*) Roeschke with which it is most apt to be confused.**

KEYWORDS: Coleoptera; Adephaga; Carabidae; Cychrini; *Scaphinotus*; *Pseudonomaretus*; Pacific Northwest; threatened or endangered species

Scaphinotus mannii Wickham (Coleoptera: Carabidae: Cychrini) is an obscure species described in 1919 from four specimens collected in southeastern Washington (Wickham 1919). Despite being known for over a hundred years, until recently it has been recorded from only a few sites in southeastern Washington and one site in northeasternmost Oregon (Bergdahl 2014, Bousquet 2012, Bousquet and Larochelle 1993, Gidaspow 1973, Greene 1975, Hatch 1953, Kavanaugh and Angel 2015, Westcott et al. 2006, Wickham 1919). Due to this small range and apparent restriction to mesic riparian gallery forests in these xeric landscapes (Bergdahl 2014, Greene 1975, LaBonte et al. 2001, Larochelle and Larivière 2003, Westcott et al. 2006), *S. mannii* has been considered a potentially threatened or endangered species (e.g., Bergdahl 2014, LaBonte et al. 2001). It has received various rankings, such as "critically imperiled" (NatureServe 2021), "globally critically imperiled" or "globally imperiled and critically imperiled in Oregon" (Oregon Biodiversity Information Center 2019), and is a candidate for state threatened and endangered species status in Washington state (Washington Department of Fish and Wildlife 2021). Consequently, distinguishing this species from similar, more commonly encountered and more widespread species in its subgenus (*Pseudomaronetus* Roeschke 1907), namely *Scaphinotus regularis* (LeConte 1884) and *Scaphinotus relictus* (Horn 1881), is of greater significance than might otherwise be the case.

Characters distinguishing *S. mannii* from other species of *Scaphinotus*, especially from other members of the subgenus *Pseudonomaretus* (Gidaspow 1973, Hatch 1953, Kavanaugh and Angel

2015, Wickham 1919), were based on the modest number of specimens available from the few known sites. Surveys in 2017 and 2018 for *S. mannii* conducted by the Washington Department of Fish and Wildlife (WDFW) found this species at numerous new localities and in several new habitat types in southeastern Washington (WDFW, unpublished data). Increased awareness of potentially wider distribution of this species resulted in its detection at three sites in Idaho during surveys for terrestrial snails (LaBonte 2022). Part of the WDFW *S. mannii* survey protocol was for field staff to screen samples for the target species. Despite provision of an image-based identification aid, confident identification of possible *S. mannii* by WDFW staff and Idaho colleagues proved unexpectedly elusive. The first author's subsequent examination of the specimens acquired during the survey revealed that variation in almost any single character was such that reliance upon it could lead to diagnostic uncertainty. Some of these additional specimens revealed that a key character previously thought to unambiguously distinguish *S. mannii* specimens from those of all other related species was in fact not reliable. This presentation details this variation and provides a modification of the key from Kavanaugh and Angel (2015) along with descriptions of additional characters to enable more accurate identification of *S. mannii* specimens versus those of *S. regularis* and *S. relictus*.

Materials and methods

For this study, 353 specimens were examined by the authors, using various stereomicroscopes, to assess morphological character states. This included 85 specimens of *S. mannii*, 78 specimens of *S. regularis*, and 190 specimens of *S. relictus*. Idaho specimens of *S. mannii* are deposited in the Orma J. Smith Museum of Natural History, College of Idaho, Caldwell, ID (CIDA), the Oregon and some Washington specimens are in the first author's personal collection (JRLC), and most of the specimens collected during the WDFW surveys are deposited in the Maurice T. James Entomological Collection, Washington State University, Pullman, WA (WSU). Eleven specimens of *S. mannii* from Washington are deposited in the California Academy of Sciences, San Francisco, CA (CAS) collection.

Measurements were obtained using an ocular micrometer disc. Images were acquired by Oregon Department of Agriculture (ODA) imaging technician Joshua B. Dunlap via ODA's state-of-the-art extended depth of field imaging system. Images were taken using Canon EOS 5DSR cameras integrated with Dun, Inc.'s Visionary Digital LK and Passport II photo stacking systems and associated Camlift Controller software. Lighting for the Passport system was provided by 600 EX Speedlites, while Profoto D2 500 AirTTL lights were used for the Visionary Digital system. RAW photo files were processed on a Windows OS PC using Adobe Bridge and then stacked using Zerene Stacker software. The stacked images were edited and finalized using Adobe Photoshop CC 2018.

Results

Several of the characters distinguishing members of *S. mannii* from those of *S. regularis* and *S. relictus* in previous keys were based on the relative proportions of various body parts. Formerly, the only diagnostic character for *S. mannii* not based on relative proportions was the absence of a seta (the posterolateral seta) from each posterior angle of the pronotum (Fig. 1A), as noted by Wickham (1919) and used in the keys of Gidaspow (1973), Hatch (1953), and Kavanaugh and Angel (2015). All specimens of both *S. regularis* and *S. relictus* examined possess such setae (Figs. 1C, 1D). Gidaspow (1973) examined at least four specimens of *S. mannii* and Greene (1975)

reported on 128 specimens of this species, and neither author reported any specimen with these setae. However, the absence of these setae is not universal among the recently acquired specimens of *S. mannii*. Of the 55 specimens obtained through the Idaho and WDFW surveys, 17 (31%) had such setae (Fig. 1B), with five of these specimens possessing a seta only near the left posterior angle. Based on the existing keys, these specimens with posterolateral setae would not be identified as *S. mannii*. Our observations to date suggest that the occurrence of adults of *S. mannii* with posterolateral setae appears to be confined to an area in southeastern Washington (Fig. 2) at the northern end of the Blue Mountains in Asotin, Columbia, and Garfield counties.

To the trained eye, adults of *S. mannii* are actually very different in overall appearance from those of either *S. regularis* or *S. relictus* (Fig. 3), with the differences numerous but subtle. *Scaphinotus mannii* adults are more slender than members of the other species, particularly with respect to the pronotum. Their external form differs from that of the other two species in several additional ways and it is tempting to include most of these characters in a key to be thorough. However, couplets with too many characters are cumbersome. The couplet we provide below is modified from the key of Kavanaugh and Angel (2015) and intended to replace their couplet 3, citing the primary characters that are most reliable and easiest to assess. Discussion of additional, secondary characters aiding confirmation of uncertain specimens follows the couplet. Although both male and female genitalia are diagnostic for distinguishing these three species (see Figs. 8-10), they are rarely visible in specimens that have not had these structures exposed or extracted. Because some individuals seeking identifications may not be willing or able to undertake the necessary dissections, we present genitalic characters here only as secondary for identification.

Modified couplet 3 from Kavanaugh and Angel (2015) for distinguishing *S. mannii* from *S. regularis* and *S. relictus*

3a. Head longer and more slender, with eyes much less convex in dorsal view (Fig. 4A), labrum (Fig. 5A) with lateral lobes long and narrow, approximately twice as long as wide at the base; pronotum (Fig. 6A) narrow, widest at or near middle, with anterior angles little projected anteriorly beyond the median anterior margin and narrowly rounded; elytral striae (Fig. 7A) shallowly impressed and regular, with punctures in striae small and with most of them separated from each other by at least several times their own diameter. . . . . *Scaphinotus mannii* Wickham

3b. Head shorter and broader, with eyes much more convex in dorsal view (Figs. 4B-C), labrum (Figs. 5B-C) with lateral lobes shorter and broader, no more than about 1.5 times as long as wide at the base; pronotum (Figs. 6B-C) broad, widest distinctly anterior to middle, with anterior angles slightly to distinctly projected anteriorly beyond the median anterior margin and broadly rounded; elytral striae (Figs. 7B-C) deeply or very deeply impressed and regular or irregular, with punctures in striae larger and closer together, more-or-less coalescent in some striae 4

Couplet 4 in the key by Kavanaugh and Angel (2015) goes on to distinguish adults of *S. regularis* and *S. relictus*.

Several additional characters are also useful for distinguishing adults of *S. mannii* from those of *S. regularis* and *S. relictus*. As noted by Gidaspow (1973), the apical stylomeres of the ovipositor in *S. mannii* females (Fig. 8A) are longer and narrower than those of either *S. regularis* (Fig. 8B) or *S. relictus* (Fig. 8C) when viewed from their broadest dorsolateral perspective. Those of

S. mannii females are about 2.5 or more times as long as broad (measured as shown in Fig. 8)) but only about twice as long as broad in females of the other two species.

In *S. mannii* males (Figs. 9A-B), the median lobe of the genitalia is narrower, with the ventral margin more evenly curved throughout and the apex more gradually narrowed in lateral view. In dorsal view (Fig. 9A), the lateral margins of the median lobe are gradually and evenly curved throughout and the lobe is smoothly narrowed to the apex. Both *S. regularis* (Figs. 9C-D) and *S. relictus* (Figs. 9E-F) males have median lobes that are thicker, with the ventral margin unevenly curved (either more abruptly deflected ventrally near the apical one-fourth (Fig. 9D) or nearly straight in the apical two-thirds (Fig. 9F)) and more abruptly narrowed apically in lateral view. In these males, the median lobe is more parallel-sided or with the lateral margins less evenly curved throughout and the lobe is slightly constricted before the apex in dorsal view (Figs. 9C and 9E). The apex of the median lobe in *S. mannii* males (Fig. 10A) is longer, slightly narrower, and with a longer apical opening (orifice). In males of *S. regularis* (Fig. 10B) and *S. relictus* (Fig. 10B), the apex is shorter, slightly to distinctly more triangular, and with a shorter apical opening.

As noted above, the posterolateral setiferous pores of the pronotum are absent (Fig. 1A) from adults of *S. manni* in most localities, but present in at least some adults from four localities in southeastern Washington (Fig. 1B). These setae are present in all specimens of *S. regularis* (Fig. 1C) and *S. relictus* examined (Fig. 1D).

Finally, there are slight differences in the proportions of protarsomeres 1-4 between males of *S. mannii* and those of the other two species. All four of these tarsomeres are relatively longer and slightly narrower in *S. mannii* males (Fig. 11A) than in males of the other species. This is particularly evident for tarsomere 1. In *S. mannii* males, the ratio of length/width = 1.4 or slightly more, whereas in males of *S. regularis* (not shown) or *S. relictus* (Fig. 11B), the length/width ratio of tarsomere 1 is 1.0 or less. We observed no significant differences in female protarsi among these species.

Discussion

A total of 217 specimens of *S. mannii* have been examined by the present and all previous authors (Hatch 1953, Gidaspow 1973, Greene 1975, and Wickham 1919). Of these, only seventeen (about 8%) are known to have posterolateral pronotal setae. The percentages of specimens examined from sites where any individuals exhibited this feature varied from 8-100% (see Table 1). Frankly, we were surprised to find any specimens of *S. mannii* with these setae present, but all of them were from newly discovered populations, each of which (except from the Charley Creek site, where only a single specimen was found) included individuals both with and without these setae. In addition, at two of the four sites at which any individuals with posterolateral setae were found, a total of five specimens (29% of all specimens with these setae) had only a single seta, and its location was on the left side in all five specimens. The Cold Creek Canyon site had one individual with a single seta and the Cummings Creek site had four. These sites are adjacent and occupy the westernmost part of the known range of this species (Fig. 2). Our sample size is small, so we cannot determine how frequent or exclusive this presence of a seta on only the left side may be in these populations, but we know of no other case of such an apparent asymmetry described among carabid beetles.

In our experience, the presence or absence of the large primary setae at midlateral and posterolateral positions along the pronotal margins in *Scaphinotus* is typically invariant within a species, except perhaps for occasional aberrant individuals in which a seta is absent unilaterally. This makes the variation seen in *S. mannii* populations somewhat perplexing. The significance of

TABLE 1. Localities at which *Scaphinotus mannii* Wickham has been found to occur.
* = site reported by Gidaspow (1973) for which we examined no specimens.

Site name	Coordinates (°N, °W)	Specimens examined	Specimens with posterolateral setae
Chimney Creek (ID)	46.0662, -116.9345	1	0
Dry Gulch (ID)	45.3666, -116.6312	1	0
Slate Creek (ID)	45.6396, -116.1296	1	0
Troy (OR)	45.9468, -117.4516	1	0
Asotin (WA)*	46.3363, -117.0602	?	0
Cold Canyon Creek (WA)	46.2242, -117.7212	13	2
Charley Creek (WA)	46.2859, -117.3129	1	1
Cummings Creek (WA)	46.2985, -117.6395	16	12
Grande Ronde Bridge (WA)	46.0721, -117.0078	4	0
Lower Joseph Creek (WA)	46.0386, -117.0066	1	0
Sheep Gulch (WA)	46.4643, -117.2373	9	0
Steptoe Canyon (WA)	46.4685, -117.1859	27	0
Tumalum Creek (WA)	46.3369, -117.6172	6	2
Wawawai (WA)	46.6347, -117.3695	4	0

this instability of the posterolateral setae in *S. mannii* is unknown, as is its genetic basis, if any. All members of all other *Pseudonomaretus* species apparently possess posterolateral pronotal setae, suggesting that this character state may be ancestral (plesiomorphic) within that subgenus and, therefore, that its loss in *S. mannii* may be derived (apomorphic). However, based on three different methods of phylogenetic analyses of nucleotide sequence data, Culpepper (2011) found members of subgenus *Pseudonomaretus* most closely related to either subgenus *Brennus* Motschulsky, 1965 or subgenus *Stenocantharus* Gistl, 1834. All members of both of these subgenera lack posterolateral pronotal setae, so it is equally likely their absence is ancestral for a group including these three subgenera and its presence in all *Pseudonomaretus* except *S. mannii* is derived. Analysis of an expanded taxon sample would be required to test this hypothesis. Also, a phylogeographic analysis of genomic data for populations of *S. mannii* alone or including the other *Pseudonomaretus* species could help to better understand the history and significance of this setal variation.

Surveys for potentially threatened or endangered invertebrates are necessary to acquire data, such as distribution, habitat, and phenology, critical to their conservation. A major challenge for invertebrate conservation surveys is the identification of target taxa. The species diversity is often overwhelming. For instance, about 460 species of Carabidae have been documented from Washington alone (Bousquet 2012). Furthermore, target taxa often closely resemble more common relatives. Other than for charismatic groups (e.g., butterflies and dragonflies), the taxonomic resources needed for support of surveys are often wanting. Often there are no other identification tools except for technical scientific publications, and for many groups, not even those exist. Invertebrate taxonomic authorities are few and far between and may not represent some taxa at all. Such authorities are often unavailable to support conservation surveys requiring examination of numerous specimens due to their primary research, academic, or other obligations. This paucity of taxonomic resources as a limiting factor for surveys and other activities requiring invertebrate identification has been referred to as the "taxonomic bottleneck" (Kim and Byrne 2006).

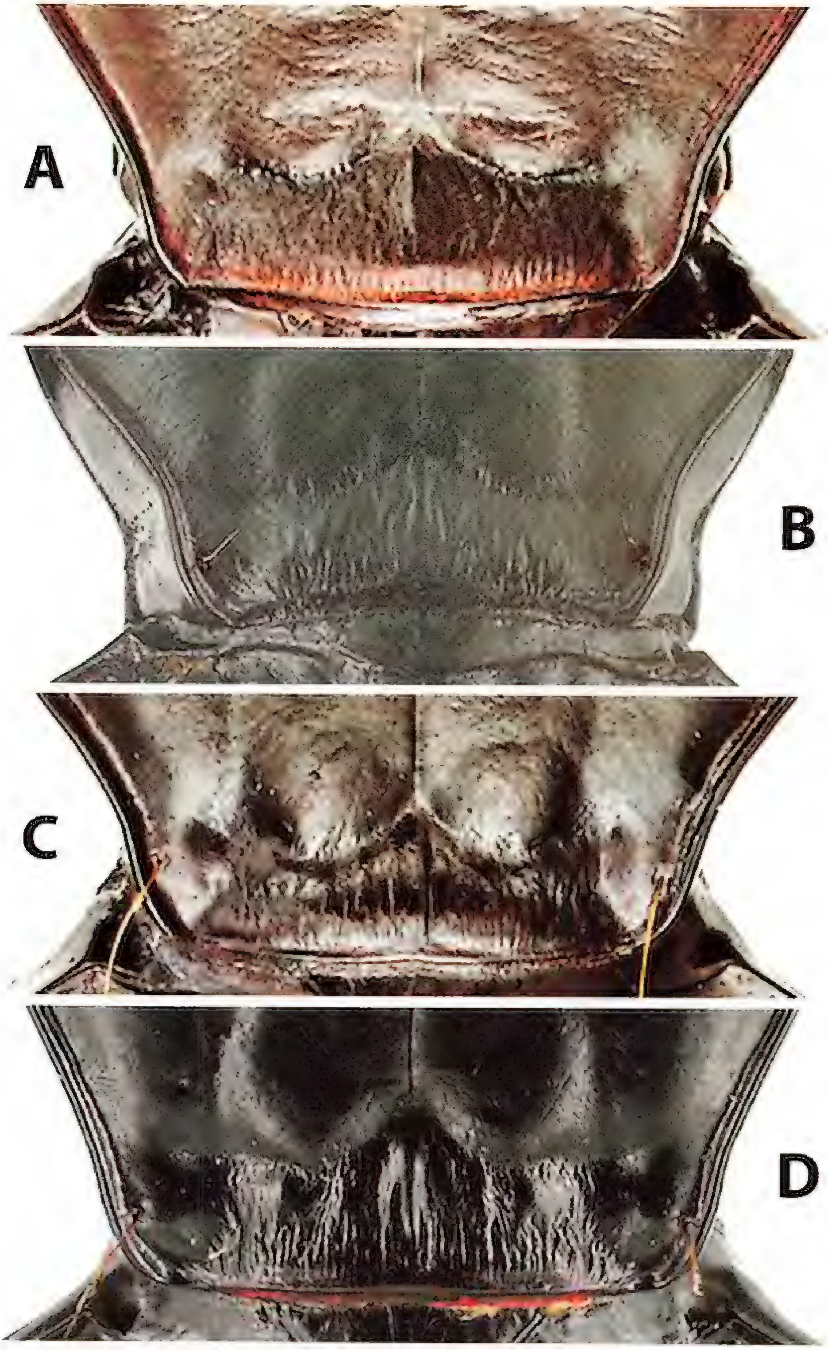

FIGURE 1. Base of pronotum showing presence or absence of posterolateral setae, dorsal view. A. *Scaphinotus mannii* Wickham with setae absent (Steptoe Canyon, Whitman County, Washington); B. *S. mannii* with setae present (Tumalum Creek, Garfield County, Washington); C. *S. regularis* (LeConte) (Slate Creek, Idaho County, Idaho); D. *S. relictus* (Horn) (8 km NNE of Moscow, Latah County, Idaho).

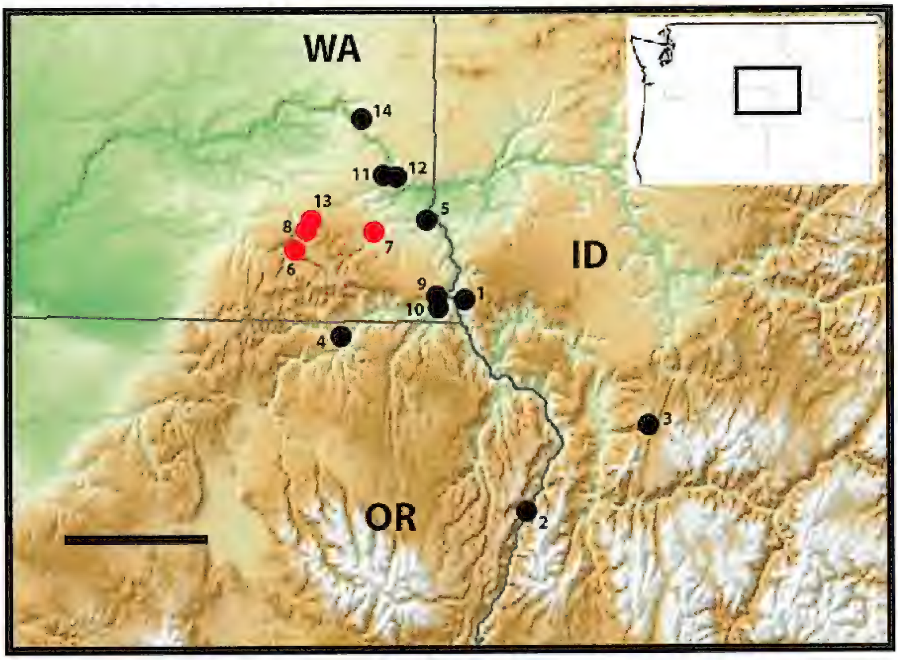

FIGURE 2. Localities for *Scaphinotus mannii* Wickham. Black dots = sites from which all specimens examined lack posterolateral pronotal setae; red dots = sites from which one or more specimens examined possess posterolateral pronotal setae. 1 = Chimney Creek (ID); 2 = Dry Gulch (ID); 3 = Slate Creek (ID); 4 = Troy (OR); 5 = Asotin (WA); 6 = Cold Canyon Creek (WA); 7 = Charley Creek (WA); 8 = Cummings Creek (WA); 9 = Grande Ronde Bridge (WA); 10 = Lower Joseph Creek (WA); 11 = Sheep Gulch (WA); 12 = Steptoe Canyon (WA); 13 = Tumalum Creek (WA); 14 = Wawawai (WA). Scale line = 100 km.

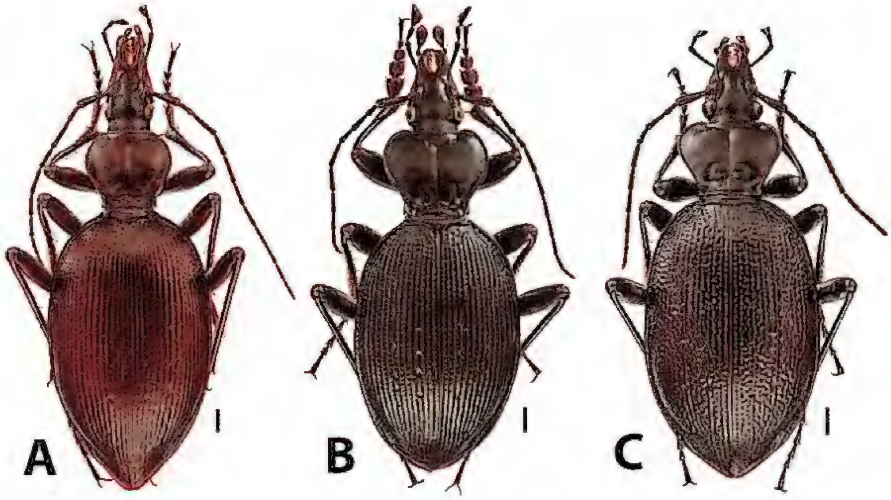

FIGURE 3. Dorsal habitus. A. *Scaphinotus mannii* Wickham (Steptoe Canyon, Whitman County, Washington); B. *S. regularis* (LeConte) (9 km SSE of Lowell, Idaho County, Idaho); C. *S. relictus* (Horn) (8 km NNE of Moscow, Latah County, Idaho). Scale line = 1.0 mm.

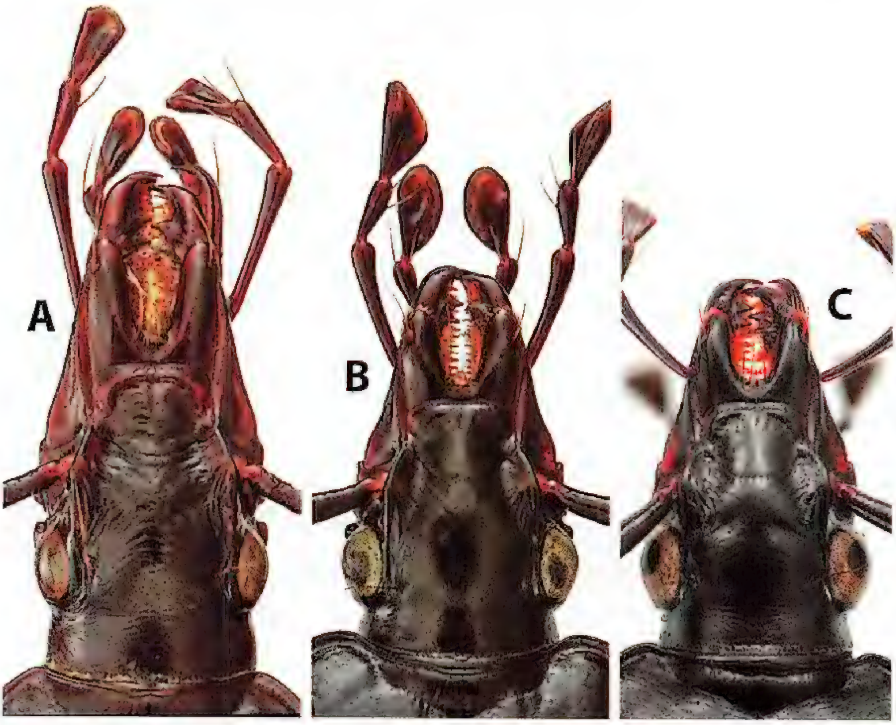

FIGURE 4. Head, dorsal view. A. *Scaphinotus mannii* Wickham (Steptoe Canyon, Whitman Co., Washington); B. *S. regularis* (LeConte) (9 km SSE of Lowell, Idaho County, Idaho); C. *S. relictus* (Horn) (Cold Creek Canyon, Columbia County, Washington).

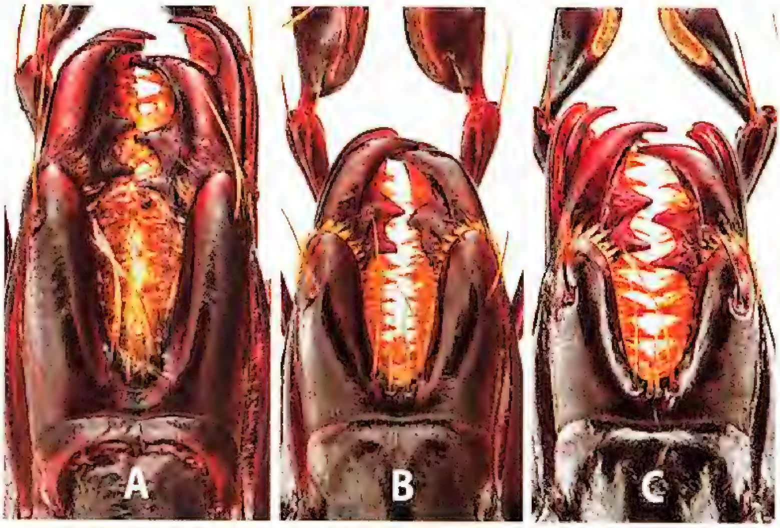

FIGURE 5. Labrum, dorsal view. A. *Scaphinotus mannii* Wickham (Steptoe Canyon, Whitman County, Washington); B. *S. regularis* (LeConte) (9 km SSE of Lowell, Idaho County, Idaho); C. *S. relictus* (Horn) (8 km SE of Craigmont, Lewis County, Idaho).

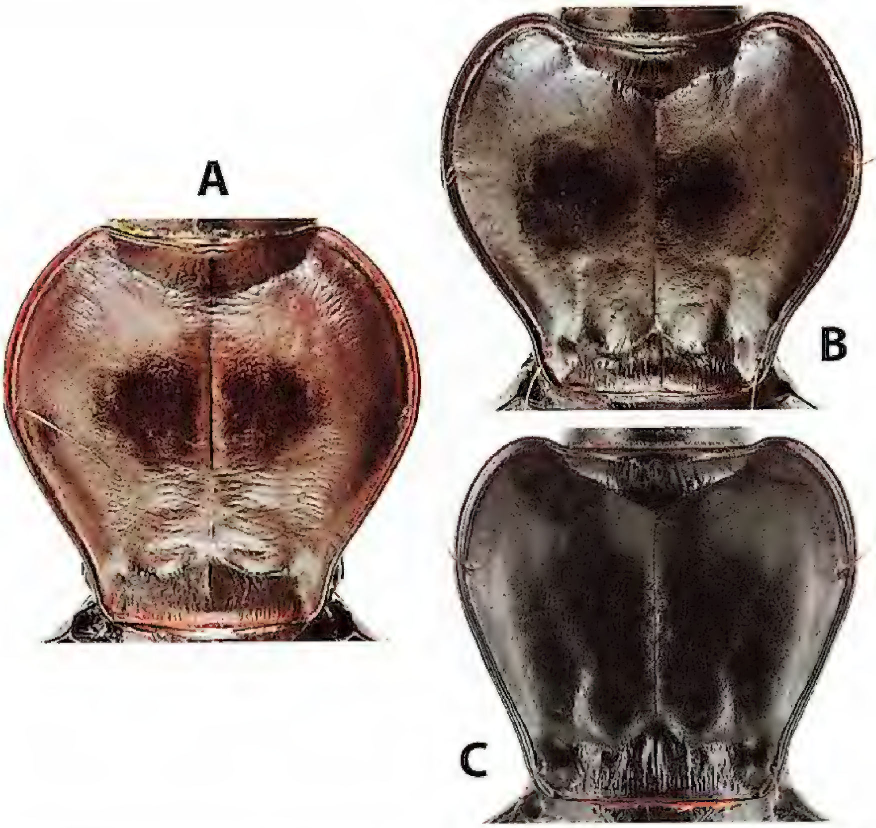

FIGURE 6. Pronotum, dorsal view. A. *Scaphinotus mannii* Wickham (Steptoe Canyon, Whitman County, Washington); B. *S. regularis* (LeConte) (9 km SSE of Lowell, Idaho County, Idaho); C. *S. relictus* (Horn) (8 km NNE of Moscow, Latah County, Idaho).

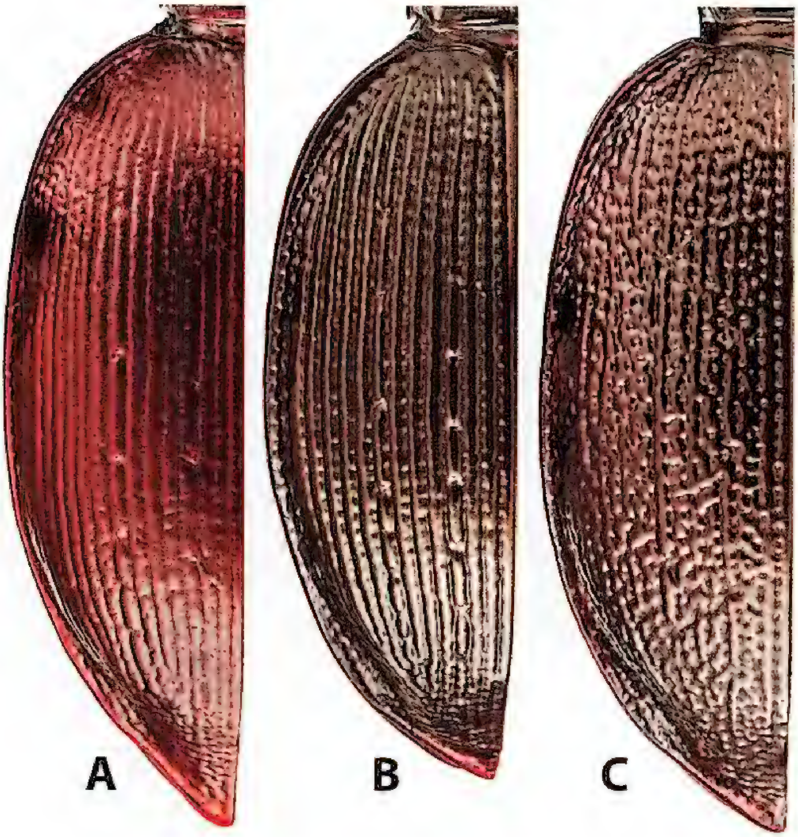

FIGURE 7. Left elytron, dorsal view. A. *Scaphinotus mannii* Wickham (Steptoe Canyon, Whitman County, Washington); B. *S. regularis* (LeConte) (9 km SSE of Lowell, Idaho County, Idaho); C. *S. relictus* (Horn) (8 km NNE of Moscow, Latah County, Idaho).

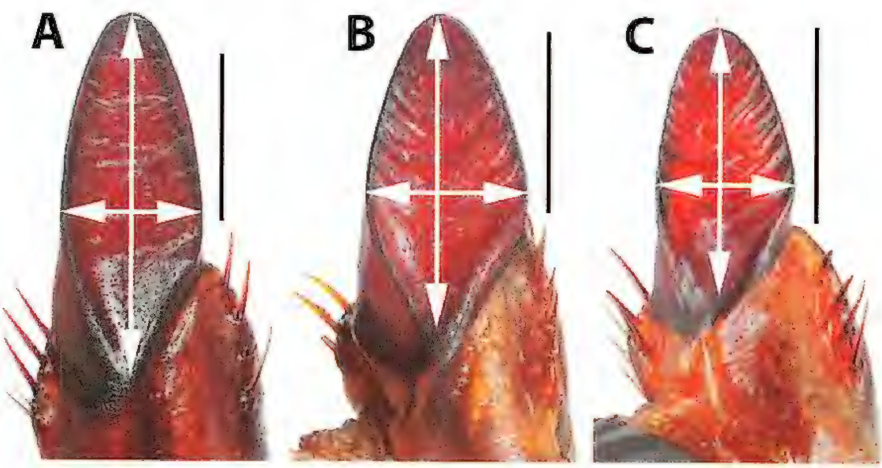

FIGURE 8. Left apical stylomere of female ovipositor, dorsolateral view. A. *Scaphinotus mannii* Wickham (Cummings Creek, Garfield County, Washington); B. *S. regularis* (LeConte) (Cambridge, Idaho County, Idaho); C. *S. relictus* (Horn) (Cummings Creek, Garfield County, Washington). Arrows indicate where length and width measurements were taken. Scale line = 0.5 mm.

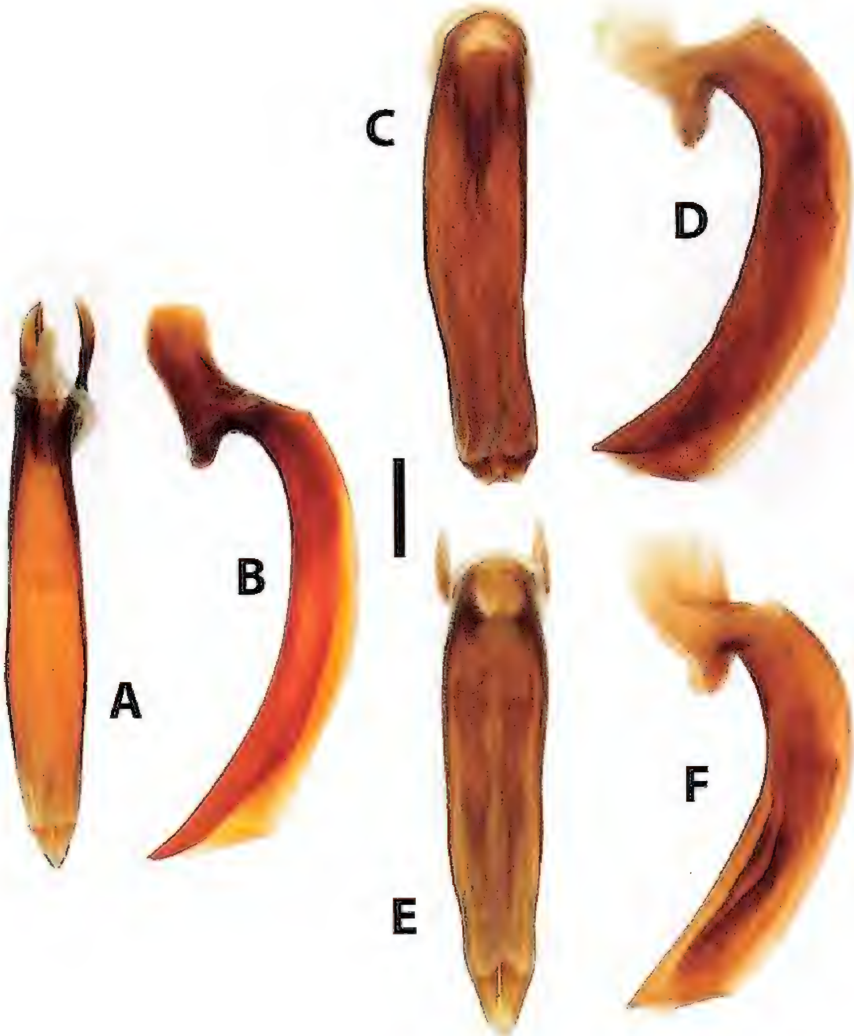

FIGURE 9. Median lobe of male genitalia. A,B. *Scaphinotus mannii* Wickham (Wawawai, Whitman County, Washington); C,D. *S. regularis* (LeConte) (Moscow Mountain, Latah County, Idaho; E,F. *S. relictus* (Horn) (Mount Spokane, Spokane County, Washington); A,C,E = dorsal view; B,C,F = left lateral view. Scale line = 1.0 mm. Images modified and reproduced with permission from Kavanaugh & Angel (2015).

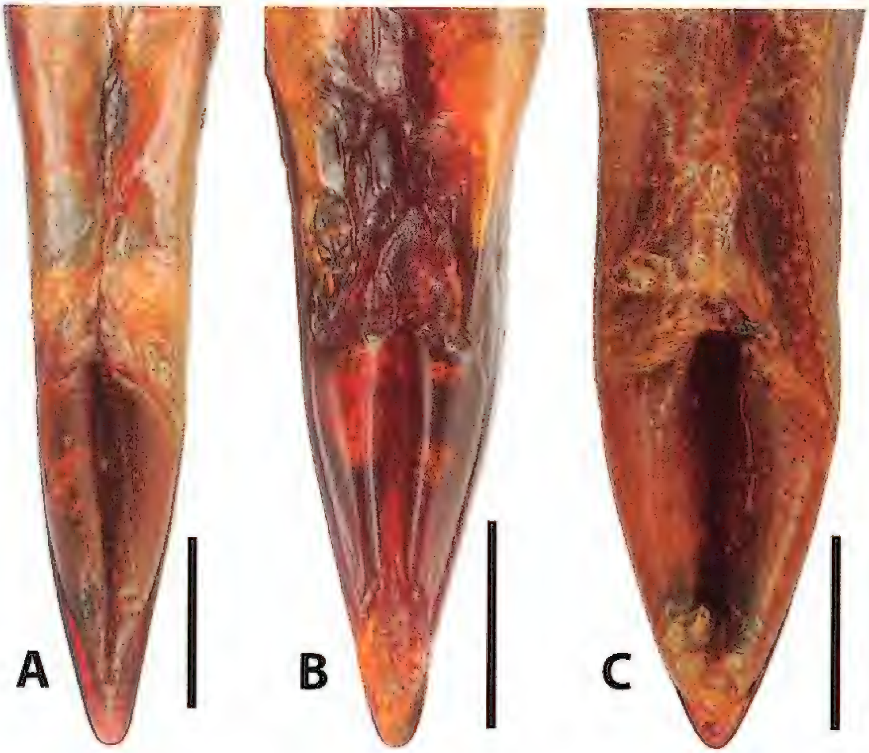

FIGURE 10. Apex of median lobe of male genitalia, dorsal view. A. *Scaphinotus mannii* Wickham (Tumalum Creek, Garfield County, Washington); B. *S. regularis* (LeConte) (9 km SSE of Lowell, Idaho County, Idaho); C. *S. relictus* (Horn) (Charley Creek, Asotin County, Washington). Scale line = 0.5 mm.

Even if published taxonomic tools are available, there are still major hurdles for non-specialists to clear. Among the barriers to invertebrate identification by non-taxonomists, such as those frequently involved in insect conservation surveys, have been the technical jargon used in keys and the housing of most comparative material in academic collections. The advent of digital photography and extended-depth-of-field (EDF) imaging as used in this paper have come far to bridge this "taxonomic abyss". While some species remain distinguishable only through examination of genitalia or DNA analysis, for many it is now possible to devise identification aids usable by a much wider audience. Characters formerly described only by paragraphs of dense and opaque technical terminology and illustrations can now be depicted as seen on a specimen. Such images also reduce reliance upon taxonomic jargon and make it much easier to understand. Digital images and EDF also limit the need to access collections for comparative material to understand characters or ensure accuracy of preliminary identifications. However, it is still essential to have all critical identifications confirmed by a taxonomic authority and to retain voucher specimens.

The suite of the primary characters presented above distinguish this species from other members of subgenus *Pseudonomaretus*, including those which are most similar, *S. regularis* and *S. relictus*. We have endeavored to produce an identification aid that will be usable by non-taxonomists, especially those in conservation and land-management agencies, as well as by professional taxonomists. It is our hope that there will be many other efforts in this vein in support of invertebrate conservation.

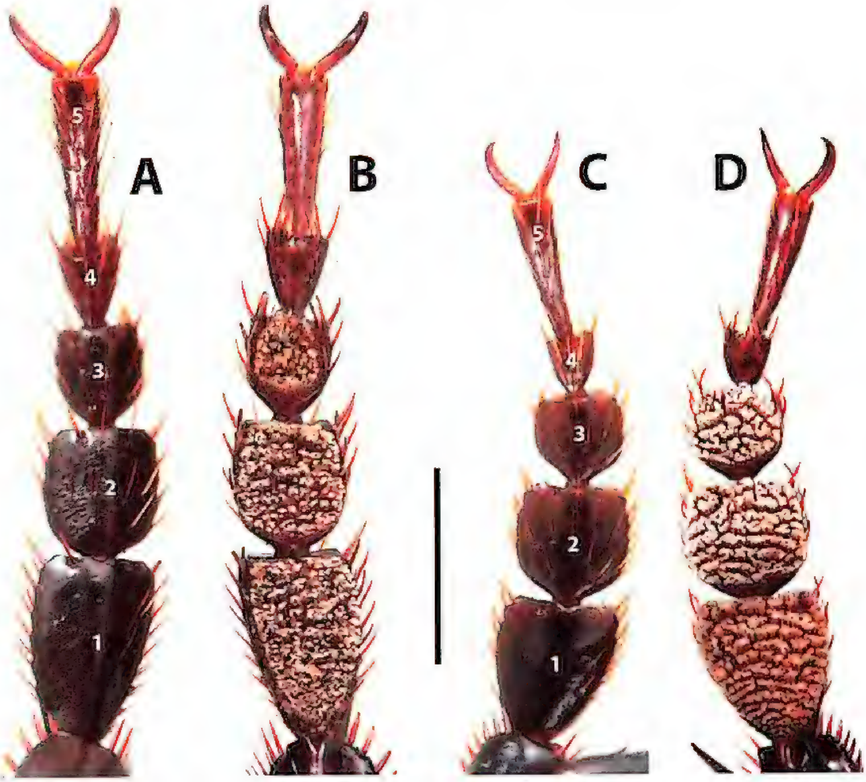

FIGURE 11. Male left protarsi, with tarsomeres (1 to 5) identified by number. A,B. *Scaphinotus mannii* Wickham (Steptoe Canyon, Whitman County, Washington); C,D. *S. relictus* (Horn) (Selway River at O'Hara Campground, Idaho County, Idaho); A,C = dorsal view; B,D = ventral view. Scale lines = 1.0 mm. Images modified and reproduced with permission from Kavanaugh & Angel (2015).

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A New Species of *Bavayia* (Squamata: Diplodactylidae) from the Loyalty Islands

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A small species of diplodactylid gecko of the genus *Bavayia* is described from Maré, the southernmost of the main Loyalty Islands chain, immediately to the east of the New Caledonian mainland. It is a member of the *Bavayia sauvagii* complex of geckos and is distinguished from its Grande Terre (mainland) relatives by its smaller size and distinctive row of precloacal pores. It is the 13th known member of the genus and joins *B. crassicollis* as the second Loyalty Islands endemic. The cause of the new species' restriction to Maré is unknown but may relate to the island's geological distinctiveness and/or to prevailing ocean currents. Another gecko restricted to Maré and surrounding islets, *Gehyra georgpotthasti*, has its affinities with Vanuatu.

Bavayia Roux, 1913 is one of eight genera of diplodactylid geckos that are endemic to the New Caledonian region, with 12 species currently recognized (Bauer and Sadlier 2000; Bauer et al. 2008, 2012a). Members of the genus occur throughout the mainland (Grande Terre) and on all offshore islands that support adequate vegetation to provide foraging opportunities. Species of *Bavayia* are extremely conservative in morphology and color pattern. Although specimens referable to *Bavayia* were first reported in 1869 (Bavay 1869) and described in the following decades (Günther 1872; Bocage 1873; Sauvage 1879; Boulenger 1883), the genus was only erected by Roux in 1913. Roux recognized only two species, *B. sauvagii* (Boulenger, 1883) and *B. cyclura* (Günther, 1872), each with subspecies. These two species form the basis of what, today, are considered to be species groups within the genus. Members of the former group are generally smaller, more gracile, and are characterized by the claw of digit I placed lateral to a single apical adhesive scansor or between a large medial and much smaller lateral scansor, a single row of precloacal pores, and a white or brown venter, whereas members of the latter group are larger, more robust, have the claw of digit I lying within a cleft in an asymmetrically divided scansor, two or three rows of pores, and have yellow venters. *Bavayia sauvagii* group species also often utilize terrestrial retreat sites under logs or in rock crevices, whereas *cyclura* group taxa are usually more strictly arboreal, although there are exceptions.

Beginning with the work of Sadlier (1989) and Bauer (1990), new species of *Bavayia* were described or raised from subspecific status and, over the course of the intervening decades, a series of additional species, mostly fairly distinctive in morphology, have been described (Bauer et al. 1998, 2008, 2012a; Wright et al. 2000). Concomitant with morphological studies of *Bavayia*,

molecular phylogenetic studies (Bauer and Jackman 2006; Bauer et al. 2012b; Skipwith et al. 2016; Bernstein et al. 2021) have revealed that many more candidate species exist and a major revision of the genus, describing 28 new taxa supported both by genetic data and morphology is currently being finalized for submission (Bauer et al., in prep.). However, one these new taxa, a species from the Loyalty Islands, lacks genetic data but is geographically and morphologically distinctive and we here take the opportunity to formally describe it.

The Loyalty Islands constitute the Province des Îles Loyauté, one of three provinces in New Caledonia. The islands lie on the Loyalty Ridge parallel to the long axis of the Grande Terre of New Caledonia, separated from it by an average of about 110 km across the Loyalty Basin, which has a maximum depth of about 2000 m. The main Loyalties extend 215 km from Ouvéa (160 km^2) in the northwest of the archipelago, through Lifou (1150 km^2), to Maré (650 km^2) in the southeast (Fig. 1). The raised rims of the islands are uplifted Pliocene to Quaternary atolls, with lower elevation interior regions representing an older (Miocene) limestone platform. Maré is distinctive in having the highest point (138 m) in the Loyalties and in having small areas of basaltic outcrops, remnants of the volcanic base upon which the Miocene reefs were built (Maurizot et al. 2020). Precipitation is low compared to the New Caledonian mainland (1300–1700 mm/yr; Maitrepierre 2012) and the vegetation is also comparatively depauperate with fewer than 400 plant species (Jaffré 1993), mostly similar to the coastal strand vegetation and inland humid forests of the Grande Terre (Däniker 1931; Schmid 1981).

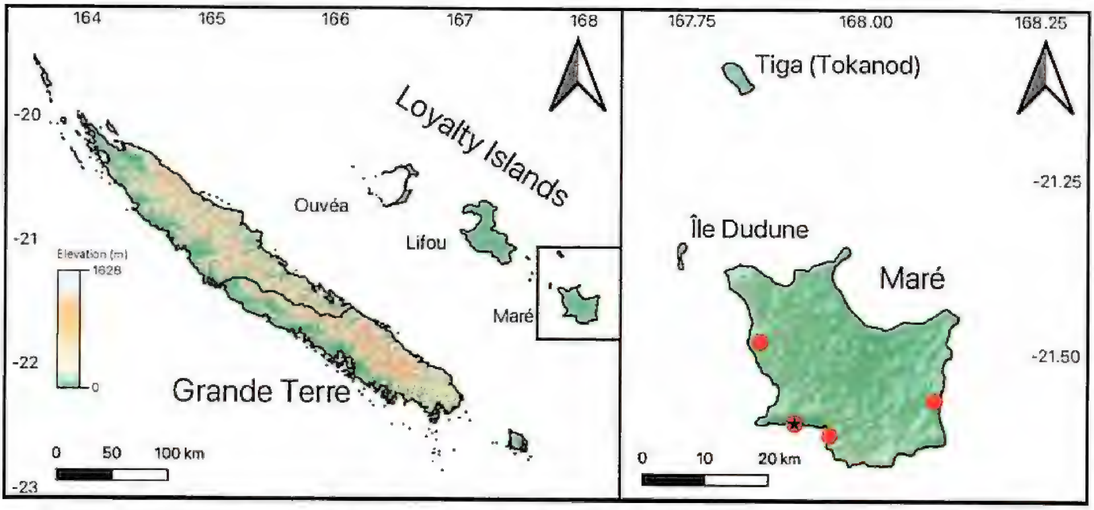

FIGURE 1. Map of New Caledonia and the Loyalty Islands (left)with enlargement of Maré and adjacent islets showing distribution of *Bavayia loyaltiensis*. Star indicates type locality, dots indicate other vouchered locations. Cartography by Jonathan DeBoer.

The herpetofauna of the Loyalty Islands has been understudied, but its composition is nonetheless reasonably well known (Sadlier and Bauer 1997; Bauer and Sadlier 2000; Flecks et al. 2012; Daza et al. 2015). *Bavayia* spp. were first recorded from the Loyalties by Roux (1913) who recognized two forms of *B. cyclura*, the nominate form and a subspecies, *B. cyclura crassicollis* (now *B. crassicollis*) from Lifou and Maré, and reported *B. sauvagii* from Maré only. Subsequent research (Bauer and Jackman 2006; Bernstein et al. 2021; Bauer et al., in prep.), has revealed that only one member of the *B. cyclura* group, *B. crassicollis*, occurs in the Loyalties and that it is an endemic that is present on all three main islands. It has also been found in 3000 year old deposits on Tiga (Tokanod), a small (10 km^2) island between Maré and Lifou, where it is certainly still pres-

ent, although uncollected, today, and reported anecdotally from Île Dudune, a small satellite off of northern Maré. To date, however, *B. sauvagii* group geckos have only been found on Maré. No *Bavayia* spp. are present on Île Walpole, 160 km ESE of Maré (Sadlier et al. 2019).

Our research on *Bavayia* has shown that the majority of species are microendemics, with individual taxa inhabiting only small portions of New Caledonia. The occurrence of a morphologically distinctive *B. sauvagii*-like gecko restricted to Maré, isolated from all other members of its species group, is an extension of this pattern of speciation in the region. Unfortunately, vouchered collections of this species do not appear to have been made subsequent to 1987 (Sadlier and Bauer 1997) and no tissue samples are available to compare it to its many named and unnamed congeners. However, a review of available material in the context of a genus-wide revision reveals that it is unambiguously diagnosable from all other described taxa (and from all soon-to-be-described taxa).

Materials and Methods

Specimens from the collections of the Australian Museum (AMS), California Academy of Sciences (CAS), Muséum National d'Histoire Naturelle, Paris (MNHN), and Naturhistorisches Museum Basel (NHMB) were examined using a Keyence VHX 6000 digital microscope. Measurements were taken with Brown and Sharpe Digit-cal Plus digital calipers. The following measurements were recorded for each specimen (see Table 1): snout-vent length (SVL); trunk length, measured between the limb insertion midpoints (TrunkL); forearm length, from elbow to wrist (ForeaL); shank length, from kneed to ankle (CrusL); tail length (TailL); tail width at base (TailW); head length from retroarticular process of mandible to snout tip (HeadL); maximal head width (HeadW); maximal head height (HeadH); maximal dimension of ear opening (EarL); orbital diameter (OrbD); distance from nares to anterior margin of orbit (NarEye); distance from snout tip to anterior margin of orbit (SnEye); distance from posterior border of orbit to anterior margin of ear (EyeEar); distance between nostrils (InterNar) and distance between the anterior margins of the orbits (InterOrb). Measurements were recorded for the right side only. Meristic data recorded (see Table 1) were midbody scale count (MidbodSCR), supralabial scales (SupraL), infralabial scales (InfraL), internasal scales (IntNas), Subdigital lamellae of the manus (ManusLam) and pes (PesLam), and number of precloacal pores. Counts of interorbital scales and scales across the narrowest point of the frontal bone are reported for the holotype only. Left (L) and right (R) counts are provided for labial scales and subdigital lamellae). Subdigital lamellae were counted from the basalmost plate that was at least twice the width of a typical scale beneath the metacarpals or metatarsals and included the terminal, undivided scansor. In the case of digit I, the paired apical plates were not included in lamellar counts (note that the method of counting used here is not identical to that used by us in earlier *Bavayia* papers, e.g. Wright et al. 2000, Bauer et al. 2008, 2012a but has been adopted here as being less ambiguous than alternative methods).

Although we prefer to use an integrative taxonomic approach (*sensu* Padial et al. 2010), the lack of genetic material for the new species forces us to rely on morphological comparisons. However, as this description is a satellite to a comprehensive and integrative review of the genus *Bavayia* in its entirety, our assessment of distinguishing features was made in the context of variation across all congeners. Adopting a general lineage species concept (de Queiroz 1999) we interpret the presence of diagnostic morphological features as evidence of lineage independence and, therefore, describe the *Bavayia sauvagii* group species endemic to Maré as a new species.

TABLE 1. Mensural and meristic features of the type series of *Bavayia loyaltiensis*. All tails are partly regenerated. See Materials and Methods for character abbreviations.

	Holotype	Paratypes								
Character	MNHN-RA 2022.0037	AMS R.125763	AMS R.125767	AMS R.125768	AMS R.125776	AMS R.125777	AMS R.125802	AMS R.125811	AMS R.125823	CAS 38826
Sex	male	female	female	male	female	male	male	male	male	male
SVL	44.9	45.1	44.1	39.6	43.0	43.3	41.4	40.5	40.0	36.7
TrunkL	20.2	18.9	20.0	16.7	20.2	19.6	17.1	18.1	16.7	15.1
ForeaL	5.7	5.0	5.3	5.0	5.7	5.4	4.3	4.7	4.8	5.9
CrusL	6.5	5.3	6.4	5.7	6.1	6.2	5.7	6.0	6.0	6.5
TailL	45.0	34.5	42.1	36.7	33.5	41.6	38.9	35.5	31.6	35.1
TailW	5.0	4.7	5.1	4.5	5.1	4.6	4.1	4.2	4.4	4.1
HeadL	12.9	13.4	12.5	12.5	13.3	13.1	12.8	12.9	12.3	13.4
HeadW	8.7	8.2	8.3	8.0	8.7	8.2	8.3	7.9	7.7	8.2
HeadH	5.3	5.1	4.7	4.7	5.0	4.8	5.0	4.6	5.0	5.0
EarL	1.1	1.4	1.2	1.2	1.3	1.0	1.0	1.0	0.8	1.1
OrbD	2.7	2.8	2.5	2.6	2.5	2.8	2.3	2.6	2.8	2.6
NarEye	3.7	3.9	3.9	3.4	3.6	3.3	3.6	3.5	3.7	3.7
SnEye	5.0	4.9	4.7	4.5	4.9	4.5	4.8	4.7	4.9	5.1
EyeEar	3.5	2.9	3.2	2.7	3.3	2.8	2.9	3.0	3.1	3.2
InterNar	1.3	1.7	1.7	1.4	1.5	1.7	1.4	1.6	1.6	1.7
InterOrb	1.9	2.0	1.8	2.0	2.1	2.0	2.2	2.1	2.0	2.1
MidbodScR	139	133	140	145	135	135	143	134	131	137
SupraLab (L/R)	11 L/ 12 R	11 L/11 R	11 L/9 R	11 L/9 R	10 L/10 R	9 L/10 R	11L/11 R	10 L/11 R	10 L/12 R	10 L/11 R
InfraLab (L/R)	11 L/9 R	11 L/9 R	9 L/8 R	8L/ 8R	10 L/9 R	8 L/8 R	10 L/9 R	11 L/9 R	10 L/8 R	9 L/ 9 R
IntNas	5	5	5	5	5	5	5	5	5	5
ManusLam L	5-10-11-10-10	6-10-10-9-8	6-9-10-9-9	6-10-11-11-9	6-9-9-10-8	6-9-10-10-8	6-9-10-10-9	5-9-11-10-8	5-9-11-11-9	5-10-11-11-9
ManusLam R	6-10-9-10-10	5-9-10-10-10	5-9-9-8-8	6-9-10-11-9	6-8-10-10-9	5-8-9-10-9	5-9-12-11-10	6-9-9-10-9	5-8-9-10-9	4-7-11-10-10
PesLam L	6-9-11-10-10	5-9-10-11-9	5-9-10-10-9	5-9-11-11-9	6-9-9-10-9	5-8-9-10-9	6-9-10-10-9	5-8-11-11-10	5-9-11-11-10	5-10-12-11-10
PesLam R	5-10-10-10-10	5-9-11-10-10	6-9-11-10-9	6-10-11-10-10	5-10-11-12-9	5-8-10-10-9	5-10-11-11-9	6-9-11-11-10	5-8-11-11-9	5-9-11-11-9
PrclPores	23	—	—	23	—	22	24	23	24 + 1	16

SYSTEMATICS

***Bavayia loyaltiensis* sp. nov.**

Figures 2–4.

Holotype (Fig. 2A).— MNHN-RA 2022-0037 (ex. AMS R.125775) Cengeite, Maré Island, Loyalty Islands, Province des Îles Loyauté, New Caledonia, 21°36′ S, 167°54′ E, coll. H.G. Cogger and R.A. Sadlier, 19 August 1987.

Paratypes (Fig. 2B).— AMS R.125763, R.125767–68, R.125776–77, same data as holotype; AMS R.125802, R.125811, same locality and collectors as previous, 20 August 1987; AMS R.125823, same locality and collectors as previous, 21 August 1987; CAS 38826, Maré Island, Loyalty Islands, Province des Îles Loyauté, New Caledonia, coll. F. Sarasin and J. Roux, December 1911.

Referred Material (all localities in Province des Îles Loyauté).— AMS R125764–66, R.125769–74, R.125786, R.125803, R.125812–14, Cengeite, Maré Island, Loyalty Islands, 21°36′ S, 167°54′ E; NHMB 7007–22, Netché, Maré Island, Loyalty Islands, 21°29′ S, 167°51′ E; NHMB 7020–21 Medou [= Medu], Maré Island, Loyalty Islands, 21°37′ S, 167°57′ E; NHMB 7022, Penelo, Maré Island, Loyalty Islands, 21°34′ S, 168°06′ E.

Diagnosis.— *Bavayia loyaltiensis* sp. nov. is a small member of the *Bavayia sauvagii* group (maximum 45 mm SVL), characterized by its gracile body, relatively short tail, digits II–V relatively narrow, claw of digit I of manus and pes borne lateral to a single medial apical scansor, usually single row of precloacal pores occupying a distinctive scale row, large number of cloacal spur scales, dorsal pattern of four largely symmetrical, well demarcated, dark transverse markings between the limb insertions, and pale head dorsum with a pair of pale nape stripes. It is distinguished from members of the *B. cyclura* group (*B. cyclura*, *B. montana*, *B. crassicollis*, *B. robusta*, *B. goroensis*, *B. nubila* and a number of undescribed species in this group) by having the claw of digit I of the manus and pes borne lateral to a single medial apical scansorial pad (vs. in a notch within an asymmetrically divided apical scansor), having beige to brownish ventral coloration (vs. yellow ventral coloration), having a gracile habitus (vs. robust) and small size (maximum 45 mm SVL vs. >50 mm except in *B. goroensis* [max. SVL 48.6 mm]), and in usually having a single row of precloacal pores (vs. usually two or more). Within the *B. sauvagii* group it may be distinguished from *B. geitaina* by its much smaller size (45 mm vs. 72 mm maximum SVL), lower number of dorsal dark markings (4 vs. 5 between limb insertions), dorsal scale rows per tail whorl 7 (vs. 9), and absence of a dark "H" or "X"-shaped marking on parietal region; from *B. ornata* by its much smaller size (45 mm vs. 69 mm maximum SVL), shorter snout (<40% HeadL vs. >40% HeadL), shorter tail (< 110% SVL vs. >110% SVL), and absence of distinct whitish spots or small blotches on limbs; and from *B. septuiclavis* by its greater number of precloacal pores (16–25, usually >20 vs. 8–14), and predominantly transverse body markings (vs. predominantly longitudinal body markings or patternless). It differs from the similarly sized *B. exsuccida* and *B. pulchella* and several related undescribed taxa in having digit I of the manus and pes borne lateral to a single medial apical scansor (Figs. 3D–E; versus lying between a larger medial and a smaller lateral scansor) and in having transverse body markings (vs. predominantly longitudinal markings, patternless, or with a bright white "V" shaped marking on the nape), and pale markings on tail much longer than darker interspaces (vs. dark interspaces longer). *Bavayia loyaltiensis* is most similar to *B. sauvagii* and a suite of related undescribed taxa, with which it shares a similar color pattern and morphology of digit I. It differs in body size from its mainland relatives (maximum 45 mm vs. 60 mm SVL in *B. sauvagii sensu stricto* and at least 50 mm in undescribed taxa) and exhibits a distinctive differentiation of the precloacal pore-bearing scale row from the adjacent

scale rows both anterior and posterior to it (Fig. 3F; vs. no such differentiation). Male *B. loyaltiensis* also may have cloacal spurs comprising clusters of up to at least 8 enlarged scales (see Fig. 3G), whereas in *B. sauvagii* and related taxa this number may be up to 6 but is usually 3 or 4.

Description.— (based on holotype — MNHN-RA 2022-0037 (ex. AMS R.125775), an adult male; Figs. 2A, 3–4). Snout-vent length (SVL) 44.9 mm; trunk relatively long (TrunkL 45% SVL) gracile, depressed. Head oblong, large (HeadL 29% SVL), relatively slender (HeadW 67% HL), not depressed (HeadH 41% HeadL), distinct from neck; interorbital/frontal region with slight midline depression, canthus well developed; snout short (SnEye 39% HeadL), less than twice eye diameter (OrbD 21% HL). Granular scales on anterior snout approximately 2–3 times diameter of those on occipital region. Pupil vertically oriented with crenelated margins; several superciliary scales in posterodorsal quadrant of orbit conical, moderately elongate, pointed. Ear opening approximately 1.5 times higher than wide, canted slightly posterodorsally to anteroventrally; eye to ear distance greater than the diameter with of eye (EyeEar 126% OrbD). Rostral rectangular, much broader than high, no median crease, contacted posteriorly by five, roughly rectangular internasals and two slightly enlarged supranasals, contacted posteroventrally by first supralabial. Nostrils oval and anterolaterally oriented, surrounded by two postnasals, one supranasal, the rostral, and in broad contact with first supralabial. Mental subtriangular, approximately as wide as deep; a single elongate, median, septagonal postmental in narrow contact with apex of mental, separating first infralabials form one another; first infralabials each in contact posteriorly with median postmental and one (L) or two (R) smaller lateral postmental chin shields. First 4–5 rows of chin shields larger than remaining throat scales. 11 L, 12 R enlarged supralabial scales, of which 7th–11th (L) and 8th–12th (R) beneath the eye; 11 L, 9 R infralabial scales; 48 interorbital scale rows between superciliaries at midpoint of orbit, 18 interorbitals between the orbital margins of the frontal bone.

Dorsal scales small, homogeneous, very slightly conical, granular; ventral scales slightly larger than dorsals, juxtaposed anteriorly becoming subimbricate and somewhat enlarged posteriorly on the body. Posterior abdominal scales rounded, mid-abdominal scales elongate, diamond-shaped. Approximately 139 scale rows around midbody. Scales of the limbs not differing from dorsals. Scales on palms and soles smooth, flattened. Precloacal pores variable in size, in a single scale row of 23 pored scales, clearly set off from the anterior scale rows and the single following scale row. Forearm and crus relatively short (ForeaL 13% SVL, CrusL 14% SVL); axillary pockets shallow. Digits long and moderately narrow, all bearing claws, those on digit I of both manus and pes reduced and partially sheathed; relative length of digits of manus: IV~III>II~V>I, and of pes: IV~V>III>II>I; digits weakly webbed; digits III and IV of pes tightly bound along length of elongate metatarsals. Subdigital lamellae typically paired, except variably single or fragmented at the base of digits. Distalmost lamella of digits II–V, manus and pes, undivided. Claw of digit I positioned lateral to a single apical scansor. Lamellar counts from right side of holotype 6-10-9-10-10 manus and 5-10-10-10-10 pes.

Tail 45.0 mm (distal ~26 mm regenerated), approximately 100% of snout-vent length, tapered, stout, roughly cylindrical in cross-section; tail base at cloacal spurs swollen. Caudal scales small, flat, rectangular, arranged in regular rows. Surface of tail weakly segmented, caudal scale rows forming whorls, each whorl 7–8 dorsal scale rows and 6 ventral scale rows long; midventral caudal scales not enlarged. Scales on pygal portion of tail one third to one half size of those on postpygal tail. Cloacal spurs consisting of five large, compressed, flattened, conical, posterodorsally directed scales, just posterolateral of the colaca.

Color in preservative: Dorsum and flanks mottled light brown with small, irregularly distributed darker brown markings, with a bold pattern of four medium brown, wavy transverse markings

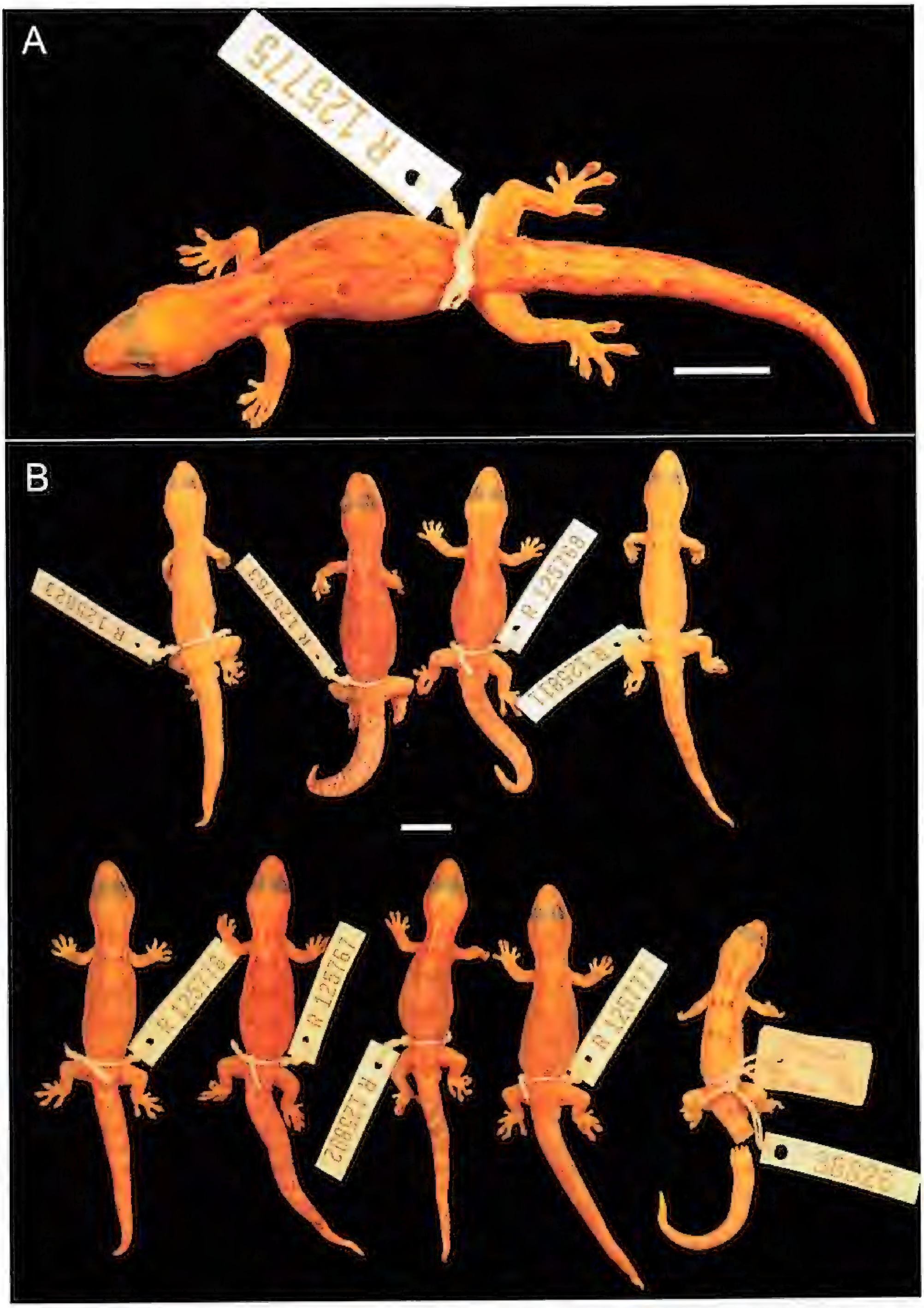

FIGURE 2. *Bavayia loyaltiensis* sp. nov. A) Holotype, MNHN-RA 2022-0037 (ex. AMS R.125775). B) Paratype series. Scale bars = 10 mm.

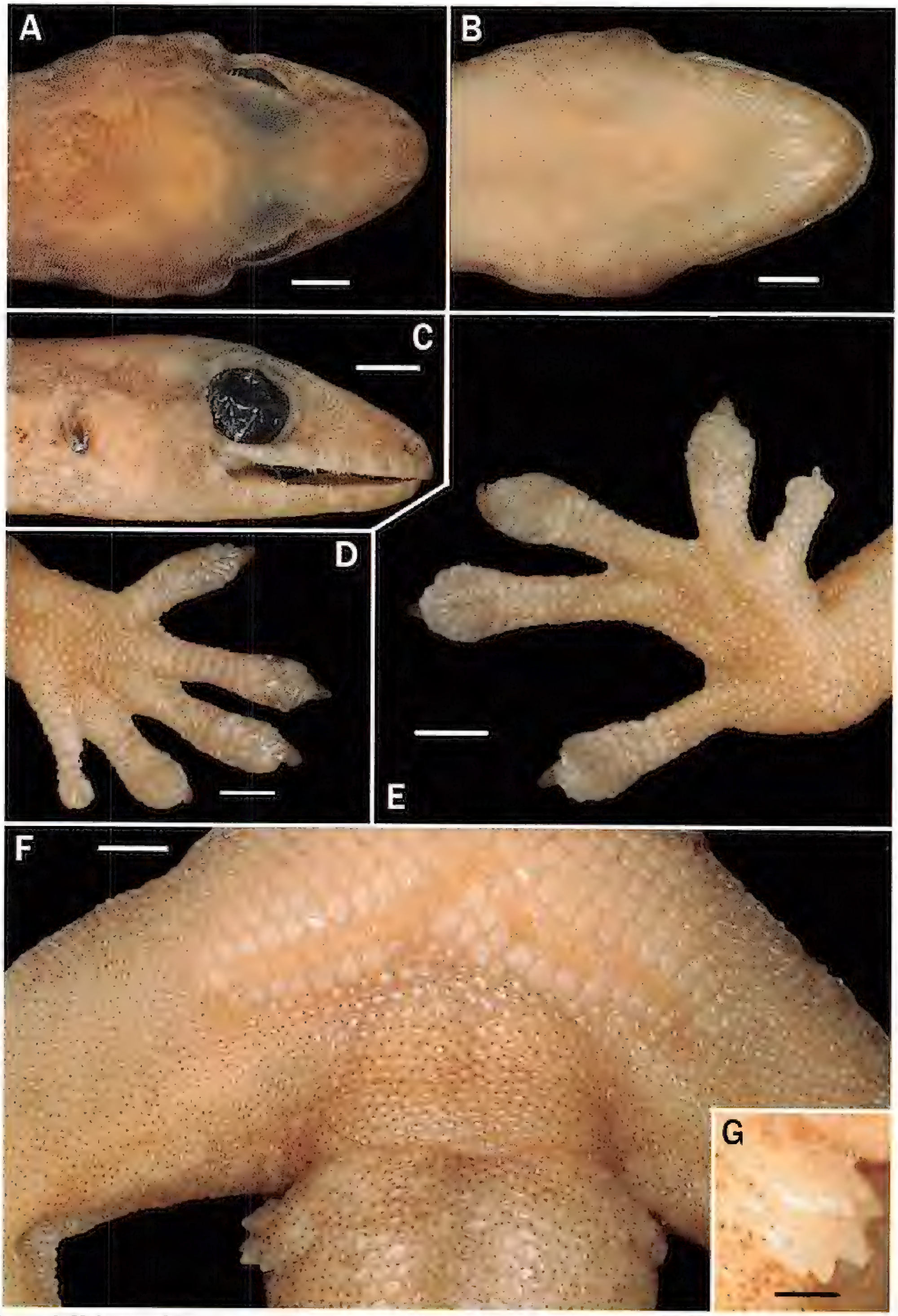

FIGURE 3. Holotype of *Bavayia loyaltiensis* sp. nov. (MNHN-RA 2022-0037). A) Dorsal view of head. B) Ventral view of head. C) Lateral view of head. D) Right manus. E) Right pes. F) Cloacal region showing distinctive pore-bearing scale row and closacal spurs. G) Close up of left cloacal spure of paratype AMS R.125811 showing the diagnostic large cluster of enlarged scales. Scale bars A–C = 5 mm, D–F = 1 mm, G = 0.5 mm.

FIGURE 4. *Bavaya loyaltiensis* sp. nov. in life. A) Holotype (MNHN-RA 2022-0037). B) Paratype AMS R.125776. Photos courtesy of H.G. Cogger.

between the limb insertions, each with scattered small, ill-defined buff spots along its anterior margin, especially evident at the lateral extremes of the dark markings. These markings each preceded by a pale blotch with vague lateral and anterior margins. Additional dark markings present on the sacrum and extending on to the postaxial margins of the thighs as a thin line, and on the nape, appearing as a medial marking and a pair of lateral ones, separated from one another by a pair of bifurcating buff-colored longitudinal stripes. Buff neck stripes converge posteriorly to form the pale blotch anterior to the first dark transverse markings of the trunk (i.e., at the shoulder). Anteriorly the buff stripes curve inward to meet the posterolateral corners of a large buff area on the parietal table. The area enclosed by the stripes laterally and the parietal anteriorly is darkest and narrowest posteriorly, becoming much lighter and quadrupling in width anteriorly yielding a bulb-shaped outline. The sides of the neck, lateral to the buff stripes, are a very diffuse brown and this coloration extends forward across the lower temporal region, through and beneath the eye and on

to the snout, although anterior to the orbit it is incomplete in places. The dorsum of the head bears some faint, irregular markings formed by individual darker granules or small clusters of granules; a faint irregular blotch is present over the nasal bones and continues to the tip of the snout as a thin wavy dark line. The margins of the orbit are pale with some diffuse whitish markings; the labial scales are brown with scattered pigment-poor areas yielding a whitish spotting on the margins of the jaw. The sides of the head posterior to the orbit and ventral to the temporal streak are densely spotted with ill-defined whitish to cream spots, which continue posteriorly on to the flanks. The largest and most conspicuous longitudinal row of such spots extends from the ventral margins of the temporal streak, over the forelimb insertions, down the flanks, over the hindlimb insertions and on to the ventrolateral margins of the original tail. Limbs similar to ground color of trunk, with irregular, faint, scattered medium brown markings. The pygal portion of the tail bears a cream to buff-colored dorsal marking that traverses the tail base constriction and extends on to the first segment of the postpygal tail. This is bordered posteriorly by a thin, broken, border of medium brown and then by a pale brown interspace that is shorter than the cream marking. Two similar markings and a portion of a third continue on the original portion of the tail, with each cream marking with irregular, but mostly symmetrical shape and with a faint brown central marking. The regenerated tail is predominantly buff with irregular, ill-defined medium brown dashes. Body venter beige with darker pigmentation under the limbs, around the cloaca, at the body margins and on the chin and throat. Subcaudal surfaces light to medium brown with scattered beige to cream markings.

Color in life.— Based on images (Fig. 4) of the holotype and a paratype (AMS R.125776) in life. Ground color grayish- to pinkish-brown with very small dark brown and white granules and clusters of granules interspersed. Dorsal dark transverse bars dark brown, each with a thin (one granule wide) anterior margin. Dorsal pale blotches and streaks on neck and temporal region grayish brown. Lateral spots bright white; larger, more prominent dorsal series extending from behind eye to sacrum. Ventral series of smaller spots running from posteroventral aspect of orbit, below ear and above forelimb insertion to flanks; anteriorly this row of spots is in series with white spots on the supralabials. Snout dark brown; orbital rims pale yellowish; iris coppery. Limbs and lower sides of neck light brown, with neither grayish- or pinkish-undertones, similar to flanks at ventrolateral margins. Tail grayish-brown to gray. Original portion of post-pygal tail bearing gray dorsal blotches with dark brown margins, alternating with mottled gray-brown interspaces. Regenerated portion of tail gray with scattered, irregular, dark brown longitudinal lines and dashes.

Variation.— Mensural and some meristic features of paratypes are presented in Table 1. All paratypes with 5 internasals contacting the rostral. First infralabials separated behind the mental in all paratype except AMS R.125776 (in contact) by an enlarged median postmental chin shield. Collectively, the first infralabials border 2–5 (usually 3) enlarged chin shields. Midbody scale rows 131–145 (mean 137). Male paratypes with a single row of ~16–24 precloacal pores (except AMS R.125823 in which there is a single median pored scale in a second row); no pores or dimpled scales in females. Cloacal spurs up to eight enlarged scales on each side (e.g. AMS R.125811). Subdigital lamellae vary contralaterally within individuals as well as between individuals; usually 5–6 under digit I of both manus and pes and a maximum of 12 under the longest digits. All specimens have partly regenerated tails, a common condition among *Bavayia* spp. Longest regenerated tail 100% SVL (holotype). Color pattern very conservative, differing among the paratypes primarily in the boldness, extent and continuity of the dark markings of the trunk, and the nape and head markings. In paratypes with more complete original tails as many as 10 pale tail markings are present (e.g., AMS R.125802).

Etymology.—Named for the Loyalty Islands (Îles Loyauté), to which the species is restricted.

Distribution.— Restricted to Maré, the southernmost island of the Loyalties (Province des

Îles Loyauté). It is possible that it may occur on the nearby islands of Tiga (Tokanod) and Dudune (Fig. 1).

Natural History.— The species occupies daytime retreats under exfoliating tree bark (Fig. 5) and has been found active on building walls on Maré (Sadlier and Bauer 1997).

FIGURE 5. Habitat of *Bavayia loyaltiensis* in forest near the Trou de Bone, southern Maré.

Conservation Status.— *Bavayia loyaltiensis* meets the criteria (B1ab(ii, iii, v) + 2ab(ii, iii, v)) to be categorized as Vulnerable on the IUCN Red List. The species is endemic to Maré Island in the Loyalty Islands and has a very small distribution with an estimated extent of occurrence of 650 km^2. It is presumed to have suffered past declines in population size and extent of occurrence as a result of loss of forest habitat from clearance for occupation and agriculture. It is considered to be at a high level of threat from further loss and degradation of forest habitat from clearance for agriculture and settlement, from predation by cats, and from the introduced Fire Ant *Wasmania auropunctata*, which has the potential to displace geckos from ground sheltering sites and arboreal foraging sites, and to affect the abundance and composition of invertebrate prey (Jourdan et al. 2001).

Remarks.— This species has previously been consistently included within *Bavayia sauvagii sensu stricto* (Roux 1913; Bauer and Vindum 1990; Bauer and Henle 1994; Sadlier and Bauer 1997; Bauer and Sadlier 2000). Roux (1913) noted the small size of specimens from Maré (SVL 45 mm) relative to *B. sauvagii* from the Grande Terre which is, in fact, diagnostic for this species. Subfossil material from Tiga may be referrable to this species (Daza et al. 2015). Recent collections are lacking from Tiga, but its proximity to Maré makes the occurrence of *B. loyaltiensis* plausible, at least historically.

DISCUSSION

The description of *Bavayia loyaltiensis* is one small step in the taxonomic recognition of the true diversity of *Bavayia* within the New Caledonian region. The composite nature of *B. sauvagii* has been suspected for at least 25 years (Sadlier and Bauer 1997; Wright et al. 2000; Bauer and Sadlier 2000). Bauer and Jackman (2006) identified previously unrecognized genetic diversity within the genus and this has recently been confirmed by Bernstein et al. (2001), who verified that barcoding data based on the CO1 mitochondrial marker was consistant with the recognition of up to 39 species. More extensive sampling based on the ND2 mitochondrial gene and several nuclear genes (Bauer et al., in prep.) has identified the same pattern and 28 new species will be described shortly. Unfortunately, no genetic material is available for *B. loyaltiensis*, so the description presented here, of necessity, relied on morphological characters only. These are sufficient to diagnose the new species and though we are unable to place the species into a molecular phylogeny,

the evidence from other congeners certainly suggests that there is geographically coherent substructure in both *B. cyclura* and *B. sauvagii*, as previously construed, that is at least heuristically supportive of the recognition of a Loyalty Islands endemic. Without molecular data we cannot be certain of the phylogenetic placement of *B. loyaltiensis* within *Bavayia*, but its morphological similarity to southern Grande Terre *B. sauvagii*, first noted by Sadlier and Bauer (1997), suggests it is a member of the clade including *B. sauvagii sensu stricto* (and two as yet unnamed species from the south of the Province Sud; Bernstein et al. 2021).

Sadlier and Bauer (1997) and Bauer and Sadlier (2000) reported nine gecko species from the Loyalty Islands. These include all of the six gekkonid geckos known from New Caledonia more generally, *Hemidactylus frenatus*, *H. garnotii*, *Hemiphyllodactylus typus*, *Lepidodactylus lugubris*, *Nactus pelagicus*, and *Gehyra georgpotthasti*. All but the last of these are also known from the Grande Terre and have been proposed to have been introduced in conjunction with human colonization, possibly as late as the arrival of Europeans in the Pacific (Grant-Mackie et al. 2003; although it is clear that on Tiga, at least *Nactus* predates European contact, Daza et al. 2015). The last species, *Gehyra georgpotthasti* is certainly native and was recently recognized (Flecks et al. 2012) to be one of several terrestrial squamates in the Loyalties with affinities to Vanuatu, to the north and east, not to the New Caledonian mainland.

With respect to diplodactylid geckos, which make up the majority of New Caledonian regional geckos, three species were earlier recognized in the Loyalties (Sadlier and Bauer 1997; Bauer 1999; Bauer and Sadlier 2000). Two of these have since been found to be conspecific and are here recognised as *B. crassicollis*, a Loyalties endemic that accounts for all *B. cyclura* group records from the Province des Îles Loyauté (Geneva et al. 2013; Daza et al. 2015). With the recognition of *B. loyaltiensis* as an endemic species, *B. sauvagii* is removed from the Loyalty Islands species list. *Bavayia loyaltiensis* joins *Emoia loyaltiensis* (Roux), *Ramphotyphlops willeyi* (Boulenger), and *Bavayia crassicollis* as the only known Loyalty reptile endemics and, with its congener, the only endemic with Grande Terre affinities. Why *B. loyaltiensis* should be restricted to Maré is unknown, although if we are correct in assuming affinities with *B. sauvagii* sensu stricto, Maré would be the closest landfall in the chain to a southern Grande Terre source population, and movement would have been facilitated by the Southern Tropical Countercurrent. Alternatively, the species may have once been more widespread in the Loyalties and may have suffered extirpation from the northern islands. *Gehyra georgpotthasti*, although of Outer Melanesian Arc affinities, has likewise reached Maré (and neighboring Dudune and Tiga, Flecks et al. 2012; Daza et al. 2015) although it seems never to have colonized Lifou or Ouvéa (a single old record from Lifou, without specific locality, is doubtful, Daza et al. 2015). While the granitic exposures of Maré make it geologically distinctive among the Loyalties, neither *Gehyra* nor *B. loyaltiensis* require, nor are even known to use, this substrate, nor, if all gekkoinids except *Nactus* are recent arrivals, would either be excluded by competitors on the more northern islands. Thus, it seems likely that the restriction in distribution reflects historical contingency.

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The Lace Web Spider Genus *Vytfutia* Deeleman-Reinhold (Araneae, Phyxelididae) in the Indo-Pacific Region

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The Indo-Pacific Phyxelididae, all members of the genus *Vytfutia* Deeleman-Reinhold, 1986, are revised. *Vytfutia bedel* Deeleman-Reinhold, 1986 from Sumatra and *Vytfutia pallens* Deeleman-Reinhold 1989 from Borneo are redescribed, and *V. labalaba*, n. sp from Borneo and *V. halandrefana*, n. sp. from Madagascar are described. Vytfutiini remain in Phyxelididae through the synapomorphies of a modified male metatarsus I and PC spigots with flattened bases crowded to encircle the anterior margin of the PMS, but differ from the Phyxelidini and Vidoleini in lacking a modified ectodistal seta on the ALS spinnerets and in lacking male epiandrous spigots.

The Phyxelididae, commonly referred to as "lace web weavers" (Jocqué & Dippenaar-Schoeman, 2006), occur in Southeast Asia, Africa from the Mediterranean to the Cape of Good Hope, and in Madagascar (Griswold, 1990, Griswold *et al.*, 2012). Adults of both sexes have a set of modified setae along the inner margin of the palpal femur (Figs. 9, 53, 54), which probably represents part of a stridulatory mechanism, and males of most species have mate clasping structures on their first (and sometimes second) legs (Figs. 27, 28, 56–61), a morphology rarely seen in araneomorph spiders. All phyxelidids are cribellate and incorporate complex, multistrand capture lines into lacey funnel or sheet webs. Ecologically they are analogous to the Amaurobiidae of the Holarctic and to the Stiphidiidae and Desidae of South America and Australasia (Wheeler *et al.*, 2016). In eastern and southern Africa (Griswold 1990) and in Madagascar (Griswold *et al.*, 2012) they are common and are the dominant terrestrial cribellate web builders. In Asia the situation is different, and phyxelidids are rare: the terrestrial cribellate niche is filled instead largely by Titanoecidae (Almeida-Silva *et al.*, 2009, 2010), Desidae and Psechridae.

Phylogenetic placement of Phyxelididae remains elusive. Lehtinen (1967) recognized the affinities of a disparate group of African taxa and placed these in his Amaurobiidae Phyxelidinae. Griswold (1990) revised the world fauna but left the phyxelidids in Lehtinen's concept of Amaurobiidae. Morphological phylogenetic studies that focused on elucidating the evolution of entelegyne spiders supported a distinct family status for Phyxelididae and suggested a sister group relationship to the Titanoecidae as part of the larger group titanoecoids (Griswold *et al.*, 1999, Griswold *et al.*, 2005). Molecular phylogenetic studies do not support the titanoecoid clade but suggest that these families, along with enigmatic Sparassidae, branch near the base of the huge "RTA clade" of primitively web-building and secondarily running spiders (Wheeler *et al.*, 2016).

Asian phyxelidids are all members of the tribe Vytfutiini, originally described as Agelenidae (Deeleman-Reinhold 1986) and only later associated with other phyxelidids (Griswold 1990).

Vytfutiini have been known from two species from rain forests and caves on two large Indonesian islands, Sumatra and Borneo (Deeleman-Reinhold 1986, 1989, Griswold *et al.,* 1999, Griswold *et al.,* 2005). Recent survey efforts in two understudied parts of the world, Wallacea and Madagascar, have revealed that the picture of Vytfutiini is both broader and richer. Through the kindness of Christa Deeleman-Reinhold, I have received a new species of *Vytfutia* from Mt. Kinabalu on north Borneo, and through the efforts of the Fisher-Griswold Madagascar Arthropod Survey Team we found another new species of *Vytfutia* from western Madagascar, extending the known range of Vytfutiini more than 6000 km across the Indian ocean.

In this revision, I summarize the synapomorphies and review the comparative morphology for the Phyxelididae and the genus *Vytfutia*, describe the two new species, redescribe and diagnose the previously known species of Vytfutiini, and provide a key to all known Vytfutiini species.

Materials and Methods

Measurements (in millimeters) were taken using a reticule in Olympus SZH, Leica MZ12.5 or Leica MZ16 stereomicroscopes; carapace length and width were taken in dorsal view, carapace height (from lower margin to dorsal midline) was taken in lateral view; leg articles were measured in lateral view along the dorsal margin. Leg measurements are depicted in species descriptions as "(Femur + Patella + Tibia + Metatarsus + Tarsus = [Total])", e.g., "II: 1.30 + 0.60 + 1.00 + 1.00 + 0.60 = [4.50]." Macrosetae are reported for the dorsal (d), prolateral (p), retrolateral (r), and ventral (v) surfaces of the legs and are listed from proximal to distal ends of each segment.

Measurements are given based on one specimen of each sex, where available: this specimen is listed at the beginning of the description. Variation for each sex is reported separately.

Photographs of somatic morphology and female genitalia were taken with a Nikon DXM 1200 digital camera mounted on a Leica MZ16A stereomicroscope. Multiple images were combined with software from Syncroscopy® or Helicon Focus®. Photographs of the epigynum in dorsal view were taken cleared in lactic acid. Illustrations of male genitalia were sketched using a camera lucida mounted on a Leica MZ12.5 stereomicroscope, rendered on coquille board, scanned and finished in Adobe Photoshop Elements®. Illustrations are by Charles Griswold.

Expansion of the male palp was accomplished by immersing it in lactic acid in a bath of water comprising a double boiler, heating to boiling on a hot plate for 5-10 minutes, and then transferring the palp to tap water where expansion of the haematodochae occurred.

Scanning electron microscopy images were taken using a Hitachi S-520, Leo 1450VP or Hitachi instrument at the California Academy of Sciences. Specimens were critical point dried, sputter coated with gold-palladium, and mounted on copper wire with white glue. A limited number of specimens were available for SEM analysis: therefore, descriptions of features based on electron microscopy (e.g., spinneret spigot morphology) may understate variation.

The sections on material examined report type and other specimens. Records are arranged by localities, specimens for each locality are summed for depository, and specimen database numbers are listed thereafter by depository. The specimen numbers assigned, e.g., CASENT…, represent identifiers for this *specimen level database* and should not be taken to imply institutional ownership of specimens. Institutional ownership by the California Academy of Sciences is denoted "CAS".

As part of the species descriptions, standard measurements were taken and ratios calculated using the following: Male palp: Length palpal tarsus; Length palpal tibia; Length of D (or DTA) / length palpal tibia; Length bulb; Width bulb; Median Apophysis (MA) length / width; MA length / bulb length; Distance to MA origin / bulb length; Male metatarsus I: distance to clasping spine

base / length metatarsus I; distance to dorsal spur base / length metatarsus I. Female genitalia: Epigynal quadrangle = width between outer margins of copulatory openings / length from anterior extent of copulatory openings to posterior margin of epigynum; Vulva length / vulva width = length of vulval capsule(s), excluding copulatory and fertilization ducts / width of outer margins of vulval capsule(s)

Species concept. I propose species hypotheses, i.e., the recognition and diagnosis of species, when I found it possible to list morphological characters that consistently distinguished entities. These species differences are expressed in a dichotomous key and these features are illustrated. Species hypotheses may be refuted if morphological feature distributions and combinations are observed to contradict the diagnoses and keys presented here.

Abbreviations and conventions. *Male palp.* C: conductor, CA: conductor apex, D and DTA: dorsal tibial apophysis, E: embolus, MA: median apophysis, RL: retrolateral lobe of tibial apex, RTA: retrolateral tegular apophysis, ST: subtegulum, T: tegulum. *Vulva.* BG: Bennett's Gland Pore (also "Dictynoid Pore"), CD: copulatory duct, CO: copulatory opening, FD: fertilization duct, LL: lateral lobe of epigynum, ML: median lobe, S: spermatheca, SA: spermathecal apex, SB: spermathecal base, SP: spermathecal poreplate. *Spinnerets.* AC: aciniform gland spigot, ALS: anterior lateral spinnerets, CR: cribellum, CY: cylindrical gland spigot, MAP: major ampullate gland spigot, mAP: minor ampullate gland spigot, MS: PLS modified spigot, n: nubbin, PC: paracribellar spigot, PI: piriform gland spigot, PLS: posterior lateral spinnerets, PMS: posterior median spinnerets, t: tartipore. *Somatic Morphology.* AER: anterior eye row, AL: anterior lateral eyes, AM: anterior median eyes, ITC: inferior tarsal claw, OA: ocular area, OAL: ocular area length, OQA: ocular quadrangle, anterior, OQP: ocular quadrangle, posterior, PER: posterior eye row, PM: posterior median eyes, PL: posterior lateral eyes, STC: superior tarsal claws. *Institutions.* CAS: California Academy of Sciences, San Francisco, Lauren Esposito, NMRL: Naturalis, Leiden, Christa Deeleman-Reinhold and Jeremy Miller.

References to figures in this paper are listed with an initial capital (Fig.); references to figures published elsewhere are listed in lower-case type (fig.).

As suggested by Agnarsson & Kuntner (2007), we consider it important to cite original descriptions in the references: the convention of not citing such original works undervalues the primary literature of taxonomy.

Taxonomy

Phyxelididae Lehtinen, 1967

Amaurobiidae Phyxelidinae Lehtinen, 1967: 328. Griswold, 1990. Elevated from subfamily of Amaurobiidae to family and placed as sister group of Titanoecidae by Griswold *et al.*, 1999: 59. Discussion in Griswold *et al.*, 2005: 35.

Diagnosis: Entelegyne, cribellate spiders with thorn-like setae located probasally on both the female and male palpal femora (Figs. 9, 53, 54), a calamistrum that originates medially on the female metatarsus IV (Figs. 8, 50), PMS paracribellar spigots that encircle the spinneret margin anteriorly and that are crowded together such that the bases are laterally flattened (Griswold *et al.*, 2005, fig. 46C) and male metatarsus I modified with apparent clasping structures (Figs. 27, 28, 56–61).

Synapomophies: Synapomorphies for the family implied by the phylogenetic analysis of Griswold, Ramírez, Coddington and Platnick (2005) were thorn-like setae located probasally on both the female and male palpal femora, a calamistrum that originates medially on the female

metatarsus IV, PMS paracribellar spigots that encircle the spinneret margin anteriorly and that are crowded together such that the bases are laterally flattened, and male metatarsus I modified with apparent clasping structures. In their analysis (Griswold *et al.*, 2005), further synapomorphies united the tribes Phyxelidini and Vidoleini: a bilaterally divided chilum and branched median tracheae. Other potential synapomorphies uniting Phyxelidini and Vidoleini include epiandrous spigots separated into two bunches (Griswold et el., 2005, figs. 160A, B) and a conspicuous, enlarged, dark seta arising laterally from the tip of the PLS (Fig. 14). *Vytfutia* have an entire chilum (Fig. 4) and lack epiandrous spigots and also lack enlarged, dark seta arising laterally from the tip of the PLS (Figs. 12, 13).

Description: (Phyxelididae) Eight eyes in two nearly straight rows (Figs. 1-4, 26, 34), canoe-shaped tapeta (Fig. 2), chilum entire (Vytfutiini, Fig. 4) or divided (Phyxelidini, Vidoleini); endite with apical serrula; sternum shield-shaped, posteriorly blunt to pointed (Figs. 21, 29, 32), labium free (Figs. 29, 33); tarsal trichobothria absent, with only a single, subapical trichobothrium on metatarsi, multiple dorsal trichobothria on tibiae, trichobothria with transverse ridges, tarsal organ capsulate with round orifice; setae plumose (Figs. 52, 53, 55), rarely (*Malaika*) also with feathery scales; palpal femora of both sexes with probasal thorns comprising enlarged setal bases and/or thickened setae (Figs. 9, 53, 54); femora to metatarsi of legs with spines (Figs. 10, 11) in most species (*Vytfutia halandrefana* sp. nov. have reduced spination); trochanters shorter than coxae (Figs. 21), trochanters unnotched or with very weak concavity (Figs. 5, 6), autospasy at coxa – trochanter joint; males of most species with metatarsus I modified (Figs. 27, 28, 56–61), median concavity typically retrolateral in African and Eurasian genera, but prolateral in Malagasy clade (*Ambohima*, *Manampoka* and *Rahavavy*), only leg I modified in most genera, legs I and II modified in *Ambohima* and *Manampoka*; leg tarsi with three claws, serrate accessory setae, claw tufts and scopulae absent (Figs. 52, 55); female palp with toothed claw (Fig. 9); metatarsi III and IV apical preening combs present (Vidoleini) or absent (Phyxelidini, Vytfutiini); calamistrum linear, originating near middle of metatarsus IV (Figs. 8, 50), calamistral setae with multiple rows of teeth or smooth (Fig. 51); lateral tracheae simple, medians simple (Vytfutiini, some Phyxelidini) or with few to many branches (Phyxelidini, Vidoleini); pedicel with lorum transversely divided (Fig. 7), epiandrous spigots grouped into two lateral bunches (Phyxelidini, Vidoleini) or absent (Vytfutiini); cribellum divided (Figs. 1213) with two fields of uniformly distributed strobilate cribellate spigots; spinnerets described in Griswold *et al.*, 2005 (figs. 46-50) female ALS with one (Vytfutiini) or two (Phxelidini and Vidoliini) MAP spigots at the inner edge and field PI spigots with round base margins, these interspersed with tartipores; female PMS with numerous (12—30) PC spigots encircling anterior margin, PC spigot bases elongate, pressed together and flattened, each PC spigot surmounted by a single strobilate shaft, spigot cuticle ridged; one large mAP spigot with nubbin and tartipore posteriad to this, posteriorly several AC and one to four CY spigots; male PMS with PC spigots replaced by encircling row of nubbins, large median tartipore and nubbin that replaces mAP spigot; female PLS with domed apical segment, with stout, curved seta apicolaterally (Phxelidini and Vidoleini), absent from Vytfutiini; with apical MS spigot, MS flanking PC or AC spigots present or absent, field of several AC and 2 or more mesal CY spigots; males lack CY spigots, MS spigot replaced by large nubbin; anal tubercle small, simple, with slender setae (Fig. 13); male palpal tibia with dorsoapical process (D or DTA) (Figs. 16, 38, 47), sclerotized (Phyxelidini, Vytfutiini) or partly sclerotized and partly hyaline (Vidoleini), additional RTA present in *Vytfutia* (Figs. 17, 37, 46); cymbium without trichobothria or chemosensory scopulae; male palpal bulbs diverse, Vytfutiini and Phyxelidini with conductor (C) and median apophysis (MA), the latter lacking in *Ambohima*, Vidoleini with three to five conical tegular processes of dubious homology; female epigyna simple, without teeth, with median (ML) and lateral (LL) lobes separate or fused

(Vytfutiini, Figs. 18, 23, 24, 39, 41, 48); vulva entelegyne, of various conformations, fertilization ducts (FD) located posterioriorly (Fig. 19); webs cribellate, may be substrate limited and radiate from retreat (Griswold *et al.,* 2005, figs. 202 A, B, E, F), or form aerial sheets (Griswold, Wood and Carmichael, 2012, fig. 2 A), spiders walk on or hang beneath webs (Griswold, Wood and Carmichael, 2012, figs 2 B, 5), cribellate silk carding type II form (carding leg braced with mobile leg IV), at least Phyxelidini wrap prey after bite with slow alternating movements of legs IV; cribellate band (studied in *Phyxelida*) entire, cribellar fibrils cylindrical with nodules, axial fibers and reserve warp present (Griswold *et al.,* 2005, figs. 121A–C).

Vytfutiini, Griswold, 1990

Type genus *Vytfutia* Deeleman-Reinhold, 1986: 34.
Comprise a single genus, *Vytfutia.*

Diagnosis, Synapomorphies and Description

See below under *Vytfutia.*

Vytfutia Deeleman-Reinhold, 1986: 34 (type species by monotypy *Vytfutia bedel* Deeleman-Reinhold, holotype male in RMNH, examined). V. Deeleman-Reinhold, 1986: 34, type *V. bedel* Deeleman-Reinhold, 1986; N.B.: transferred from Agelenidae to Amaurobiidae by Griswold, 1990: 186, to Phyxelididae by Griswold et al., 1999: 59.

Diagnosis: *Vytfutia* may be distinguished from other Phyxelididae by having the epigynum (Figs. 24, 39, 41, 48) with the posterior median lobe fused to the lateral lobes so that no suture is visible, by the presence of a retrolateral process (RL) on the male palpal tarsus and a sclerotized dorsal spur on male metatarsus I (Figs. 16, 37, 46), by the entire chilum (Fig. 4) and by the PLS lacking the stout, curved, apicolateral seta (Figs. 12, 13).

Synapomorphies: Among the Phyxelididae, the dorsal spur on male metatarsus I (Figs. 56–61), RTA on the male palpal tibia, and fusion of median and lateral sectors of the epigynum into a single plate (Figs. 24, 39, 41, 48) comprise *Vytfutia* synapomorphies.

Notes: *Vytfutia halandrefana* and *V. pallens* are the most morphologically divergent species of *Vytfutia*, and also very different to each other. *Vytfutia halandrefana* is small, with a broad thoracic fovea, few leg spines and complex female genitalia with convoluted ducts. Unfortunately, the male of *V. halandrefana* remains unknown. Vulval morphology suggests that the *V. halandrefana* male palp has an elongate embolus. *Vytfutia pallens* is much larger than other *Vytfutia*, with longer limbs and pale coloration, as befits a cave-dwelling organism.

Description: (*Vytfutia*) Total length 2.12–7.70. Markings differ significantly among species and are described under each species description. Carapace length 1.19–1.43 times width, height 0.39–0.53 width; thoracic fovea typically linear, length 0.11–0.18 carapace length, narrow oval in *V. halandrefana,* length 0.07 carapace length. PER straight to slightly recurved, AER straight, ocular area width 2.25–3.33 times length; clypeal height typically 1.20-1.70 times AM diameter, but lower in *V. halandrefana*, 0.60–0.80 times AM diameter; chelicerae with small boss (Figs. 1, 35), length 6.50–14.00 times clypeal height, pro- and retromargins of fang furrow with 3–5 heterogeneous teeth, retromargin with 3-4 escort setae at fang base, promargin with large group of fluffy whisker setae, rake setae not found (Ramirez 2014); cheliceral gland on flat cuticle, with numerous pores; labrum with flattened, anteriad pointing labral tongue, tongue apex free, deeply concave, with plumose setae dorsally and laterally on labrum, minute, bristle-like setae occur distad of tongue apex; sternum length 1.17–1.39 times width, apex a blunt point (Figs. 29, 33). Legs long, femur I 1.01–1.48 times carapace length; leg I always longest, III shortest, leg formula 1423, in some species 1243 or 1 [2=4] 3; male metatarsi I (Figs. 27, 28, 56–61) with retrolateral,

concavity at midsegment, concavity lacks spinules, at base of concavity a short, prolateral process surmounted by stout clasping spine, concavity arising at 0.21-0.47 length of metatarsus, concavity length 0.21–0.27 metatarsus, with short, dorsal spur at apex of concavity, spur height 0.06–0.95 of metatarsus length; legs otherwise unmodified; palpal claw and STC with numerous (up to 11) teeth (Figs. 52, 55), ITC with 2-3 teeth or smooth (*V. pallens*); calamistrum subapical, origin at 0.22-0.29 distance from metatarsus base, length 0.33–0.46 metatarsus length (Figs. 8, 50). Spination (following summary is based on males and females of *Vytfutia labalaba*; *V. bedel* and *V. pallens* are very similar; the female of *V. halandrefana* is very different, which is noted in that species' description). Male: palp: femur d0-1-1, p0-1-0; leg I: femur d1-1-1, p0-0-0-1, r0-0-1, tibia d0-0-1, p0-1-1-0, r1-1-1-0, metatarsus p0-0-1, v2-0-0-2, r0-1(clasper)-0; leg II: femur d1-1-1, p0-0-1-0, r0-0-1-0, tibia p0-1-1-0, r0-1-2-0, metatarsus p0-1-1-2, r0-0-2; leg III: femur d1-1-1, p0-0-1-0, r0-0-1-0, patella d0-1, p1, r1, tibia d1-0-0, p0-1-1-0, v0-0-1-0, r0-1-1-0, metatarsus p1-1-0-2, v2-0-0-2, r1-1-0-1; leg IV: femur d1-1-1, p0-0-1-0, r0-0-1-0, patella d0-1-0, tibia d1-0-0, p0-1-1-0, v0-1-1-0, r0-1-1-0, metatarsus p1-1-0-2, v2-0-0-2, r1-1-0-1. Female: palp: femur d0-0-1-1, r0-0-1; leg I: femur d0-1-1-0, p0-0-0-1, tibia p0-1-1-0, r0-1-1-0, metatarsus p0-0-1, v2-0-0, r0-0-1; leg II: femur d1-1-1, p0-0-1, r0-0-1, tibia d1-1-0-2, v2-0-0-2, r1-1-0-2, p0-1-1-0, metatarsus d0-0-1, p0-1-1-0, v2-0-0-2, r0-0-1-0; leg III: femur d1-1-0-1, p0-0-0-1, r0-0-0-1, patella p1, r1, tibia p0-1-1-0, v1-1-0-0, r0-1-1-0, metatarsus p1-1-0-2, v2-0-2-1, r1-1-0-2; leg IV: femur d1-0-0-1, p0-0-1, r0-0-1, patella d1, tibia p0-1-1-0, v1-1-0-0, r0-1-1-0, metatarsus d2-0-01, p1-1-0-2, v0-1-0-2, r0-0-0-1. Male epiandrum lacking spigots. Tracheae comprise four simple tubes that are limited to the abdomen (Deeleman-Reinhold, 1986: 34). Spinnerets (based on scanning electron microscope [SEM] examination of three species: males and females of *V. pallens* Deeleman-Reinhold (Griswold *et al.*, 2005, figs. 46D, 47, 48) and of *V. labalaba* new species and a female of *V. halandrefana*, new species). *Vytfutia* are typical phyxelidids in cribellum and paracribellar morphology, and universally differ from Vidoleini and Phyxelidini in lacking the large, stout, curved seta (black when viewed with light microscopy) at ectal margin of the PLS (compare Figs. 14 and 12). Cribellum width 0.43–0.67 spinnerets width (Fig. 12). Female ALS may have one mesal MAP spigot with a posterior MAP nubbin; *V. halandrefana* differs in retaining two MAP spigots. Piriform gland (PI) spigots in females range from as few as 18 (*V. halandrefana*) to more than 50 (*V. pallens*); males have fewer; small tartipores are scattered throughout PI spigot field; female PMS with as few as 10 (*V. halandrefana*) to more than 25 (*V. labalaba*) PC spigots; replaced by nubbins in the male; the PMS of both sexes have one anteromedian mAP spigot and at least two (*V. halandrefana*) to six (*V. labalaba*) AC spigots and one (*V. halandrefana*) to four (*V. pallens*) CY spigots; female PLS with large anterior MS spigot with cylindrical base and shaft, accompanied by a flanking AC, MS and flanking AC are replaced by nubbins in male; female with one (*V. halandrefana*) to three (*V. labalaba*) CY spigots and fewer than eight AC spigots. Palpal femur with anterobasal row of four to eight stout setae set in enlarged bases, these setae shortened and enlarged as thorns (Figs. 9, 53, 54); male palpal tibia (Figs. 16, 46, 47) with short to long, convex, simple DTA extending apically, RTA developed as a trapezoidal flange; cymbium with retrolateral paracribellar projection (Figs. 15, 38, 46, 47); palpal bulb with a small, oval petiole, anneli of subtegulum weakly developed, tegulum central, convex, course of reservoir a simple curve within bulb, without switchbacks, median apophysis present, fleshy, arising at mid-bulb near embolic base; embolus a slender, narrow, tapering blade to a slender spine, pars pendula fused basally with truncus of embolus, embolus flexibly attached to tegulum; conductor apical, fleshy, grooved to receive apex of embolus (Figs. 15, 36, 37, 45, 46). Female genitalia with epigynum (Figs. 18, 24, 39, 41) a simple, undivided plate, copulatory openings slit like, transverse, oblique to longitudinal; vulva with capsulate structures(s) with internal chambers,

with 2-3 lobes, at least *V. labalaba* with sessile HS and posterdorsal Bennett's gland pore (Fig. 42), may have convoluted ducts (*V. halandrefana*, Fig. 25).

Composition: Four species, all in the genus *Vytfutia*.

Distribution: The Indo-Pacific islands of Madagascar, Sumatra and Borneo (Fig. 62).

Key to the species of Vytfutia

1 Males **5**

— Females **2**

2 (1) Epigynum deep, quadrangle less than 1.00, copulatory opening rims oblique to nearly longitudinal, posterior margin of epigynum convex or concave (Figs. 18, 39, 48), vulva with 2-3 simple lobes, without slender ducts, vulva width greater than twice length (Figs. 19, 40, 49) **3**

— Epigynum broad, quadrangle greater than 2.50, copulatory opening rims transverse, posterior margin of epigynum concave (Figs. 23, 24), vulva complex with large anterior lobe and slender ducts, vulva width less than 1.50 times length (Fig. 25), Madagascar. . . . . ***V. halandrefana*, new species**

3 (2) Epigynum with copulatory opening rims oblique (Figs. 39, 48), vulva with integrated lobes anteriad of copulatory openings (Figs. 40, 49) **4**

— Epigynum with copulatory opening rims longitudinal, epigynum posterior margin convex, elongated posteriorly in center (Fig. 18), vulva with spherical lobe laterad of copulatory openings (Fig. 19) . . . . *V. bedel* Deeleman-Reinhold, 1986

4 (3) Epigynum with copulatory opening rims converging anteriorly, posterior margin slightly concave (Figs. 39, 41), vulva with paired lobes laterad of copulatory openings (Figs. 40, 42). . . . . ***V. labalaba*, new species**

— Epigynum with copulatory opening rims diverging anteriorly, posterior margin straight to slightly convex (Fig. 48), vulva with paired lobes far anteriad of copulatory openings (Fig. 49). . . . . *V. pallens* Deeleman-Reinhold, 1989

5 (1) Male palpal tibia with DTA short, less than 0.25 length tibia (Figs. 37, 38, 46, 49), tibia with subapical spine or cuspule, embolus short, arising near base of bulb (past 6 o'clock) and making turn of less than 180°, median apophysis long, length greater than 5.00 times width (Figs. 36, 37, 45, 46) **6**

— Male palpal tibia with DTA elongate, greater than 0.50 length tibia (Figs. 16, 17), tibia lacking subapical enlarged seta, embolus long, arising on retrolateral side of bulb (4 o'clock) and making turn of more than 225°, median apophysis short, length less than 4.00 times width (Figs. 15, 17) . . . . *V. bedel* Deeleman-Reinhold, 1986

6 (5) Palpal tibia with elongate apical spine (Figs. 46, 47), embolus short, straight, arises on prolateral side of bulb (near 8 o'clock), median apophysis hooked at apex (Figs. 45, 46); metatarsus I long, base of concavity originates at more than 0.45 metatarsus length, spur high, height great than 0.09 metatarsus length (Figs. 60, 61) . . . . . . *V. pallens* Deeleman-Reinhold, 1989

— Palpal tibia with short subapical cuspule (Figs. 37, 38), embolus long, curved, arises at base of bulb (near 6 o'clock), median apophysis flattened, spoon shaped at apex (Figs. 36, 37); metatarsus I shorter, base of concavity originates at less than 0.35 metatarsus length, spur low, height greater than 0.08 metatarsus length (Figs. 58, 59). . . . . ***V. labalaba*, new species**

***Vytfutia bedel* Deeleman-Reinhold, 1986**
Figures 15–19, 56, 57, 62

Vytfutia bedel Deeleman-Reinhold, 1986: 35 (male holotype and female paratype from Sumatra, RMNH, examined). Griswold 1990: 186. Griswold *et al.*, 2005: 90.

Diagnosis: Males with palpal tibia with DTA elongate, greater than 0.50 length tibia (Figs. 16, 17), tibia lacking subapical enlarged seta, embolus long, arising on retrolateral side of bulb (4 o'clock) and making turn of more than 225°, median apophysis short, length less than 4.00 times width (Figs. 15, 17); females with epigynum with copulatory opening rims longitudinal, epigynum posterior margin convex, prolonged posteriorly in center (Fig. 18), vulva with spherical lobe laterad of copulatory openings (Fig. 19); thoracic fovea linear.

Male (after Deeleman-Reinhold, 1986: 35): Total length 3.60. Carapace yellow-brown, ocular area and chelicerae dark brown; legs pale yellow-brown; dorsum of abdomen pale yellow with paired, dorsal dark cardiac marks, broken into anterior and median groups, transverse chevrons posteriorly. Carapace 1.70 long, 1.20 wide, carapace length 1.33 times width, carapace height 0.39 times width; PER 1.18 times AER, PER 2.36 times OAL, OAL equals OQL, OQA 0.65 times OQP; clypeal height 1.67 times AM diameter; ratio of eyes AM:AL:PM:PL,1.0:2.33:2.0:2.0, AM-AM, AM-AL equal AM diameter, PM-PM, PM-PL 0.80 times PM, AL touching PL; chelicerae 0.70 long, cheliceral length 7.0 times clypeal height; sternum length 1.22 times width; labium length equals width; palpal coxae length 1.78 times width. Legs with typical spination. Leg measurements: I: 1.70 + 0.60 + 1.50 + 1.50 + 0.70 = [6.00]; II: 1.40 + 0.60 + 1.10 + 1.20 + 0.60 = [4.90]; III: 1.20 + 0.50 + 0.90 + 1.00 + 0.40 = [4.00]; IV: 1.40 + 0.50 + 1.10 + 1.40 + 0.50 = [4.90]; palp: 0.70 + 0.50 + 0.50 + NA + 0.60 = [2.30]; femur I 1.42 times carapace width; leg formula: 1 4=2 3. Metatarsus I as in Figs. 56, 57, clasping spine barely reaches median spur, spur short, length less than ¼ segment width. Male palp as in Figs. 15–17; male palpal tibia length 0.52 times cymbial length, RTA length 0.86 times tibia, MA origin 0.27 of distance to tegular base, MA length 0.63 that of tegulum, MA length 2.71 times width. Female (after Deeleman-Reinhold, 1986: 34): Total length 4.0. Markings as in male except carapace with dark marks at margin of pars cephalica that meet at anterior of straight thoracic fovea, and with four small transverse dark marks on each side of thoracic fovea. Carapace 1.70 long, 1.30 wide, carapace length 1.31 times width, carapace height 0.53 times width; PER 1.2 times AER, PER 2.25 times OAL; OAL equals OQL, OQA 0.67 times OQP; clypeal height 1.33 times AM diameter; ratio of eyes AM:AL:PM:PL, 1.0:2.67:2.0:2.0, AM-AM, AM-AL equal to AM; PM-PM 0.67 PM, PM-PL 0.85 PM; AL-PL touching; Chelicerae 0.70 long, cheliceral length 9.25 times clypeal height; sternum length 1.17 times width; labium length 0.93 times width; palpal coxae length 1.62 width. Legs with typical spination. Leg measurements: I: 1.60 + 0.60 + 1.40 + 1.20 + 0.70 = [5.50]; II: 1.30 + 0.60 + 1.00 + 1.00 + 0.60 = [4.50]; III: 1.10 + 0.40 + 0.70 + 0.90 + 0.40 = [3.50]; IV: 1.40 + 0.60 + 1.00 + 1.10 + 0.50 = [4.60]; palp: 0.70 + 0.30 + 0.40 + NA + 0.60 = [2.00]; leg formula = 1423; femur I 1.23 times carapace width. Epigynum as in Fig. 18, epigynum width 0.75 times length; epigynum MLW equal to MLL; epigynum MLW 10 times LLW. Vulva as in Fig. 19.

Natural History: Deeleman-Reinhold (1986) stated that this species occurs in primary tropical rainforest and noted that it is rare and apparently lives in isolated clusters. Among the collecting data that she quotes are "from leaves" and ""in small irregular web in forked branch" (Deeleman-Reinhold (1986: 34)."

Distribution: Known only from the type locality in northern Sumatra (Fig. 62).

Material Examined: INDONESIA: *N. Sumatra*: Gunung Leuser, border of National Park at Bohorok in primary rainforest, Nov. 15, 1983, elev. 200 m, from leaves (Deeleman, RMNH), 1♂, 1♀ (male holotype and female paratype, *Vytfutia bedel* Deeleman-Reinhold).

Vytfutia halandrefana **Griswold, new species**
Figures 20–25, 50–55, 62

Types: Holotype female (CASENT9012513) from gallery forest along the Mandraré River in the Forêt de Bealoka, Réserve Privé Berenty, Toliara Provence, Madagascar, (24°57′25″S, 46°16′17″E, elev. 34m), collected 3–8 February 2002 by the Fisher-Griswold Arthropod Survey Team, collection code BLF5320, deposited in CAS. Paratype female (CASENT9008848) from tropical dry forest at Tombeau Vazimba, Bekopaka, Parc National Tsingy de Bemaraha, Toliara Provence, Madagascar, (19°8′31″S, 44°49′41″E, elev. 50m), collected 6–10 November 2001 by the Fisher-Griswold Arthropod Survey Team, collection code BLF4230, deposited in CAS.

Etymology: The specific name is from the Malagasy words for spider, *hala*, and west, *andrefana*, commemorating the distribution of this westernmost *Vytfutia* species; a noun in apposition.

Diagnosis: Females with epigynum (Figs. 23-25) broad, quadrangle greater than 2.50, copulatory opening rims transverse, posterior margin of epigynum concave, vulva complex with large anterior lobe and slender ducts, vulva width less than 1.50 times length (Fig. 25); thoracic fovea oval, length less than 0.08 carapace length (Fig. 20); smallest *Vytfutia*, total length of females 2.12–2.42; male unknown.

Male: Unknown. **Female** (holotype, CASENT9021513): Total length 2.12. Markings as in Figs. 20, 21, carapace and chelicerae dark brown, labium and palpal coxae yellow-brown, venter and legs yellow-white; abdomen grey-white with dorsal brown cardiac marks broken into anterior and median parts, dorsum and sides with intermixed, scattered brown spots and white guanine deposits, venter plain yellow white. Carapace 0.95 long, 0.80 wide, 0.36 high; clypeus 0.04 high, height 0.80 AM diameter; ocular area 0.18 long, 0.46 wide, OAL 1.07 times OQL; ratio of eyes AM:AL:PM:PL, 1.00:1.11:1.11:1.22, diameter of PM 0.06; AM-AM 0.89 AM diameter, AM-AL 1.22 AM; PM-PM and PM-PL 1.60 PM; AL-PL 0.18 times PL. Chelicerae 0.41 long; sternum 0.56 long, 0.50 wide; labium 0.18 long, 0.21 wide; palpal coxae 0.27 long, 0.15 wide. Femur I length 1.01 times carapace width. Spination greatly reduced compared to other *Vytfutia* species: Female: palp: femur d0-1-0, tibia d1-0-2, p0-0-1, tarsus p0-1-1, v1-1-2-2-1; leg I: femur d0-1-1-0, p0-0-0-1, tibia r0-1-1-0, metatarsus v2-0-0; leg II: femur d1-1-0, p0-0-1, tibia p1-1-0-2, r0-1-0, metatarsus v2-0-0-0; leg III: femur d10-0-0; leg IV: femur d10-0-0. Leg measurements: I: 0.81 + 0.34 + 0.72 + 0.62 + 0.56 = [3.05]; II: 0.75 + 0.31 + 0.56 + 0.50 + 0.31 = [2.43]; III: 0.72 + 0.28 + 0.44 + 0.47 + 0.31 = [2.22]; IV: 0.81 + 0.34 + 0.59 + 0.56 + 0.28 = [2.58]; palp: 0.37 + 0.12 + 0.19 + na + 0.31 = [0.99]. Calamistrum as in Figs. 22, 50, 51; palpal femur thorns as in Figs. 53, 54; tarsal claws IV as in Figs. 52, 55. Epigynum as in Figs. 23, 24, vulva as in Fig. 25. Variation (N=2): Total length 2.12–2.42; carapace length 1.19–1.25 times width, height 0.45–0.56 width; PER 1.12–1.13 times AER, 2.50–2.81 times OAL; OAL 1.04–1.07 times OQL; clypeal height 0.60–0.80 times AM diameter; cheliceral length 10.80–14.00 times clypeal height; sternum length 1.19–1.26 times width.

Natural History: Collection records from beating and pitfall trapping suggest that this species occurs on vegetation and on the ground in gallery forest and tropical dry forest.

Distribution: Known from central and western Toliara Province, Madagascar (Fig. 62).

Material Examined: MADAGASCAR: Toliara Prov., Réserve Privé Berenty, Forêt de Bealoka, Mandraré River, 14.6 km 329° NNW Amboasary, elev. 35 m, 24°57′25″S, 46°16′17″E, beating low vegetation - gallery Forest, 3–8 February 2002, Fisher-Griswold Arthropod Survey Team, collection code BLF5320 (*Holotype* Female CASENT9021513), same data (Female CASENT9012420); Parc National Tsingy de Bemaraha, 3.4 km 93° E Bekopaka, Tombeau Vazimba, 19°8′31″S, 44°49′41″E, elev. 50m, pitfall trap in tropical dry forest, 6-10 November

2001, Fisher-Griswold Arthropod Survey Team, collection code 4230 (*Paratype* female, CASENT9008848).

Vytfutia labalaba **Griswold, new species**
Figures 1–13, 26–44, 58, 59, 62

Types: Holotype male and paratype female collected on the wall of a building at 1550 m elevation on Mt. Kinabalu, Sabah-Borneo, Malaysia, by P. Zbarowski, 2–8 April 1990, deposited in Naturalis, Leiden.

Etymology: From a Malay word for spider, labah-labah; a noun in apposition.

Diagnosis: Males with palpal tibia having a short subapical cuspule (Figs. 37, 38), embolus long, curved, arises at base of bulb (near 6 o'clock), median apophysis flattened, with spoon-shaped apex (Figs. 36, 37); females with epigynum with copulatory opening rims oblique, converging anteriorly, posterior margin slightly concave (Figs. 39, 41), vulva simple, with paired lobes laterad of copulatory openings (Figs. 40, 42); thoracic fovea linear (Fig. 34).

Male (holotype): Total length 2.40. Markings as in Figs. 26–30; carapace orange-brown, darker on ocular area; chelicerae, labium and palpal coxae dark brown, sternum brown, coxae, trochanters, leg femora and palpal femur-tibia pale yellow, remainder of legs yellow-brown; palpal tibia and cymbium dark brown; abdomen pale grey with anterodorsal dark brown cardiac mark (Fig. 27), sides and venter speckled with brown, dark brown anterior to epigastric furrow and around spinnerets (Fig. 28). Carapace 1.26 long, 0.95 wide, 0.42 high; clypeus 0.07 high, height 1.20 times AM diameter; ocular area 0.18 long, 0.45 wide, PER strongly recurved, OAL equals OQL; ratio of eyes AM:AL:PM:PL, 1.00:1.33:1.33:1.42, diameter of PM 0.08; AM-AM 0.70 AM diameter, AM-AL 0.50 AM; PM-PM and PM-PL equal PM diameter; AL-PL 0.18 PL. Chelicerae 0.50 long; sternum 0.76 long, 0.54 wide; labium 0.20 long, 0.21 wide; palpal coxae 0.38 long, 0.20 wide. Legs with typical spination; femur I length 1.25 times carapace width; metatarsus I as in Figs. 58, 59, clasping spine extends beyond median spur, spur long, length greater than 1/3 segment width. Leg measurements: I: 1.19 + 0.47 + 1.12 + 1.06 + 0.59 = [4.43]; II: 1.09 + 0.44 + 0.87 + 0.87 + 0.53 = [3.80]; III: 1.00 + 0.44 + 0.69 + 0.81 + 0.47 = [3.41]; IV: 1.16 + 0.47 + 0.91 + 0.94 + 0.47 = [3.95]; palp: 0.69 + 0.16 + 0.34 + na + 0.50 = [1.69]. Palpal tibia length 2/3 cymbial length, RTA broad, apically concave, RTA length 1/4 tibia length, DTA length also 1/4 tibia length, narrow, with sharply pointed apex (Fig. 38); cymbium tapering with conical proximobasal paracymbium; tegulum with MA origin subbasal, distance to tegular base 0.19 tegular length, MA large, length 0.77 that of tegulum, oval, length five times width, margins smooth and apex expanded (Fig. 36), apex concave on bulb side (Fig. 37); base of conductor broad, fleshy, tapering to pointed apex; embolus convex, unmodified, gradually tapering to pointed apex. Female (paratype): Total length 3.25. Markings as in Figs. 1–13, 31–35, as in male except carapace and mouthparts darker (Figs. 33–35) and dorsal cardiac mark on abdomen broken into several parts, extending for whole length of abdomen (Fig. 31). Carapace 1.39 long, 1.03 wide, 0.55 high; clypeus 0.09 high, height 1.70 times AM diameter; ocular area 0.18 long, 0.52 wide, OAL equals OQL; ratio of eyes AM:AL:PM:PL, 1.00:1.10:1.60:1.40, diameter of PM 0.08; AM-AM 1.28 times AM diameter, AM-AL 1.365 times AM; PM-PM 0.73 PM, PM-PL 1.50 times PM; AL-PL 0.17 times PL. Chelicerae 0.59 long; sternum 0.82 long, 0.61 wide; labium 0.21 long, 0.24 wide; palpal coxae 0.41 long, 0.23 wide. Femur I length 1.48 times carapace width. Legs with typical spination. Leg measurements: I: 1.53 + 0.59 + 1.28 + 1.16 + 0.69 = [5.25]; II: 1.25 + 0.47 + 0.94 + 0.94 + 0.59 = [4.19]; III: 1.19 + 0.50 + 0.78 + 0.78 + 0.47 = [3.72]; IV: 1.16 + 0.56 + 0.97 + 0.94 + 0.56 = [4.19]; palp: 0.62 + 0.31 + 0.44 + na + 0.59 = [1.96]. Epigynum as in Figs. 39, 41, vulva as in Figs. 40, 42–44, with lateral double lobes that have proximal HS pores (Fig. 44) and a distal BG pore (Fig. 43).

Natural History: The holotype and paratype were collected on the wall of a building at Kinabalu Park headquarters, elevation 1550m. The collecting labels state "in ridges…outer wall bungalow" and "webbe als *Amaurobius simiis*". This suggests that this species builds a cribellate appressed sheet or funnel on objects that offer space for a retreat, as is typical of many Phyxelididae and Titanoecidae. The elevation of the type locality suggests that surrounding vegetation is lower montane rainforest.

Distribution: Known only from the type locality on Mt. Kinabalu, Borneo (Fig. 62).

Material Examined: Only the holotype male and paratype female from Mt. Kinabalu, Malaysia, in Naturalis, Leiden.

Vytfutia pallens Deeleman-Reinhold, 1989

Figures 45–49, 60–62

Vytfutia pallens Deeleman-Reinhold, 1989: ♂M♀F paratypes from Niah Cave, Sarawak, Malaysia, 10 April 1984, C. Deeleman and C. Hug, RMNH, examined. Griswold *et al.*, 2005: 90.

Diagnosis: Males with palpal tibia with elongate apical spine (Figs. 46, 47), embolus short, straight, arises on prolateral side of bulb (near 8 o'clock), median apophysis hooked at apex (Figs. 45, 46); females with epigynum with copulatory opening rims oblique, diverging anteriorly, posterior margin straight to slightly convex (Fig. 48), vulva simple, with paired lobes of spermathecae extending far anteriad of copulatory openings (Fig. 49); largest *Vytfutia* (see Figs. 60, 61), total length of males 4.40–5.00, of females 6.20–7.70; markings pale; legs long, male metatarsus I with base of concavity at more than 0.45 metatarsus length, spur high, height greater than 0.09 metatarsus length (Figs. 60, 61).

Male (paratype, after Deeleman-Reinhold, 1989: 622-623): Total length 4.40. Carapace light grey-brown, ocular area slightly darker; chelicerae dark brown; labium, palpal coxae, sternum, and legs light grey-brown; abdomen pale with 3 snowy granulations on dorsal surface. Carapace 2.20 long, 1.70 wide; carapace length 1.29 times width; PER 1.14 times AER, PER 2.28 times OAL; OAL 0.57 times OQL; OQA 0.625 times OQP; ratio of eyes AM:AL:PM:PL, 1.0:2.0:3.0:3.0; AM-AM, AM-AL equal to AM diameter; PM-PM, PM-PL equal to PM diameter; AL touching PL. Sternum length 1.26 times width; labium length 0.75 times width; palpal coxae length 2.0 times width. Legs with typical spination; femur I length 1.25 times carapace width; metatarsus I as in Figs. 60, 61, clasping spine extends beyond median spur, spur long, length nearly ½ segment width. Leg measurements: I: 2.3 + 0.9 + 2.2 + 1.9 + 1.2 = [8.5]; II: 2.1 + 0.7 + 1.8 + 1.8 + 1.0 = [7.4]; III: 2.1 + 0.8 + 1.5 + 1.7 + 0.9 = [7.0]; IV: 2.3 + 0.9 + 1.9 + 1.9 + 1.0 = [8.0]; palp: 1.2 + 0.4 + 0.6 + NA + 0.6 = [2.8]; leg formula 1423. Male palp as in Figs. 45–47; tibia length 1.21 times cymbial length, RTA length 0.23 times tibia (Figs. 46, 47), MA origin 0.36 distance to tegular base, MA length 0.83 times that of tegulum, MA length 7.86 times width (Figs. 45, 46). Variation (N=3): Total length 4.40 to 5.00. **Female** (Paratype, after Deeleman-Reinhold, 1989: 622-623): Total length 6.70. Markings as in male. Carapace 3.30 long, 2.30 wide, carapace length 1.43 times width, carapace height 0.47 width; PER 1.11 times AER, PER 2.50 times OAL; OAL equals OQL; OQA 0.59 times OQP; clypeal height 1.25 times AM diameter; ratio of eyes AM:AL:PM:PL, 1.0:1.6:1.6:1.2; AM-AM 0.6 times AM diameter, AM-AL equals AM diameter; PM-PM 1.125 times PM diameter, PM-PL 1.25 times PM, AL touching PL. Chelicerae 1.30 long; cheliceral length 12.0 times clypeal height; sternum length 1.34 times width; labium length 1.09 times width; palpal coxae length 1.75 times width. Legs with typical spination. Femur I 1.26 times carapace width. Leg measurements: I: 2.9 + 1.2 + 2.5 + 2.4 + 1.3 = [10.30]; II: 2.7 + 1.1 + 2.2 + 2.0 + 1.0 = [9.00]; III: 2.4 + 1.0 + 1.7 + 1.7 + 1.0 = [7.80]; IV: 2.7 + 1.1 + 1.9 + 1.9 + 1.0 = [8.60]; palp: 1.1 + 0.25 + 0.70 + NA + 1.0 = [3.05], leg formula 1243. Female genitalia as in Fig. 48 (epigynum)

and Fig. 49 (vulva). Epigynum width 2.66 times length; epigynum MLW 2.20 times MLL, MLW 1.50 times LLW. Variation (N=12): Total length 6.20 to 7.70.

Natural History: Deeleman-Reinhold (1989: 619, 620, 624) describes this species from Niah Cave, Sarawak, Malaysia, a cave famous for the diversity of endemic species.

Distribution: Known only from the type locality (Fig. 62).

Material Examined: Only the paratypes from Niah Cave, Sarawak, in RMNH.

Conclusions

Morphology places *Vytfutia* among the Phyxelididae (Griswold *et al.*, 1999, 2005): we find in *Vytfutia* the peculiar male metatarsus I claspers and stridulating picks inside the palpal femur of both sexes that are Phyxelididae synapomorphies. On the contrary, molecular data suggest that *Vytfutia* may fall outside of Phyxelididae. To date (end of 2021) only Griswold *et al.*, (2012: fig. 60) have included *Vytfutia* in a molecular phylogeny where it was recovered outside of other phyxelidids (Vidoleini and Phyxelidini) plus *Goeldia* (Titanoecidae). New molecular data from transcriptomes and UCE's ultraconserved sequences e.g., Fernández *et al.*, (2018), Kulkarni *et al.*, (2020) and Ramírez *et al.*, (2020), may permit precise placement of phyxelidids, and of *Vutfutia* relative to them and other spiders. Unfortunately, *Vytfutia* are rare and remain rarely collected: the Asian species are known from only three collecting events (one per species). One Asian species, *V. pallens*, was collected in caves, a typical habitat for relict species. In Madagascar, among more than 30,000 spider specimens processed, sorted, labelled and identified to family at the California Academy of Sciences from 1998-2020, only three female *Vytfutia* specimens from two collecting events have been found.

The extension of a spider clade across the Indian Ocean from Indonesia to Madagascar (but excluding Africa) is an unusual but not unprecedented biogeographic pattern. Most recent studies, e.g., Agnarsson and Kuntner (2012) and Wood and Griswold (2022), suggest that most of Madagascar's spider fauna descends ancestors that dispersed over water. As these authors note, Africa is the most important source for such ancestors, but trans-Indian Ocean patterns suggesting dispersal are also found. Phylogenetic relationships of Madagascar to Asia emerge from other studies, i.e., rock weavers (Titanoecidae: Almeida-Silva *et al.*, 2010), goblin spiders (Oonopidae: Alvarez-Padilla *et al.*, 2015), jumping spiders (Salticidae: Andriamalala, 2007), armoured spiders (Tetrablemmidae: Lehtinen, 1981) and spurred trapdoor spiders (Idiopidae: Raven, 1985). The horned jumping spiders *Padilla* were studied by Andriamalala (2007) who, using her data and those from Maddison and Hedin (2003) and Benjamin (2004), recovered *Padilla* within the Ballinae and showed affinities to Asian relatives. Her dated phylogeny suggests an origin for *Padilla* as late as the Neogene, too late for Gondwana vicariance, and suggested instead that *Padilla* reached Madagascar on island stepping stones and across long water expanses in the Indian Ocean. The discovery by Ledoux (2007) of typical *Padilla* on La Réunion Island reinforces the hypothesis of *Padilla* island-hopping. The titanoecid spider *Pandava laminata* (Thorell 1878) extends from South East Asia across the Indian Ocean to Madagascar, presaging our new records for the phyxelidid *Vytfutia*. We cannot rule out the occurrence of phyxelidids in south Asia and welcome collecting efforts in the Indian subcontinent.

I hope that we see more studies of the spider fauna extending from SE Asia to Africa, involving careful comparative morphology, taxonomy and application of the rapidly evolving techniques of molecular phylogenetics. Such measures are urgently needed to understand the evolution of phyxelidids, and of the whole circum-Indian Ocean biota.

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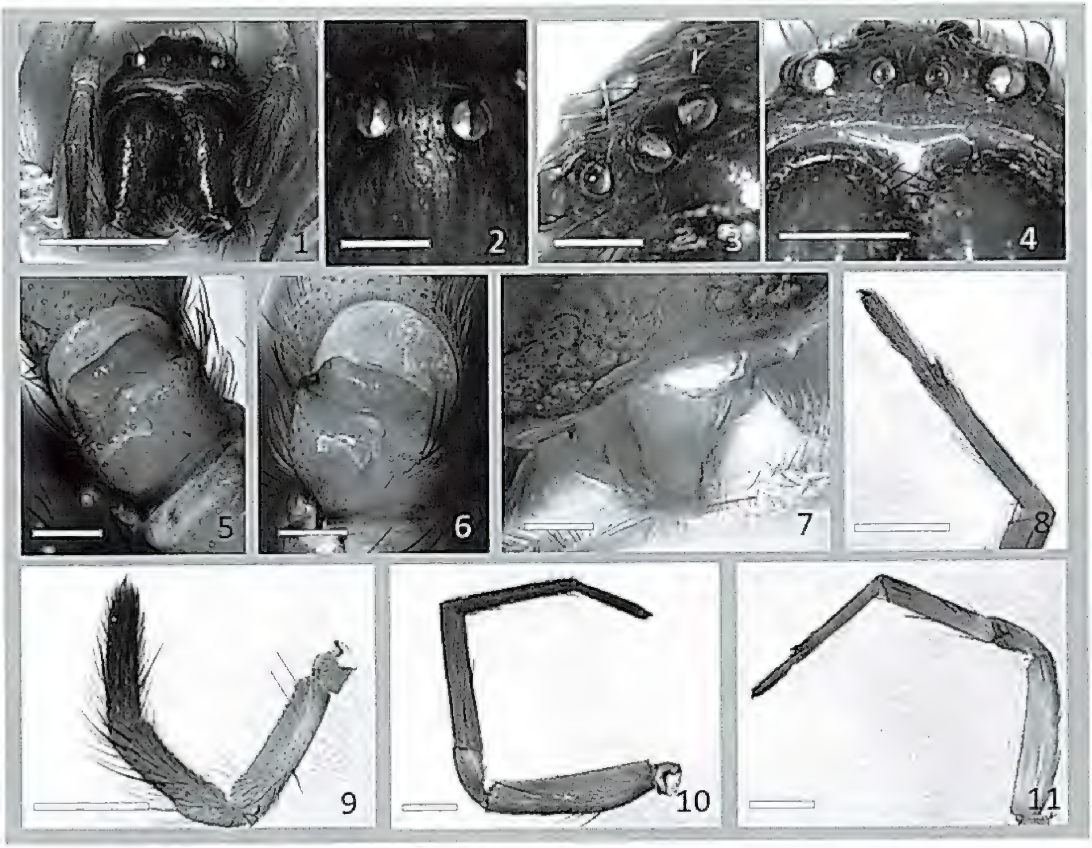
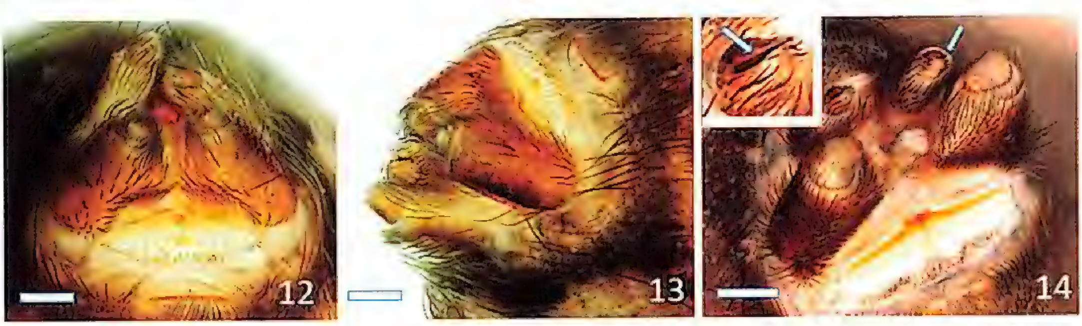
ILLUSTRATIONS

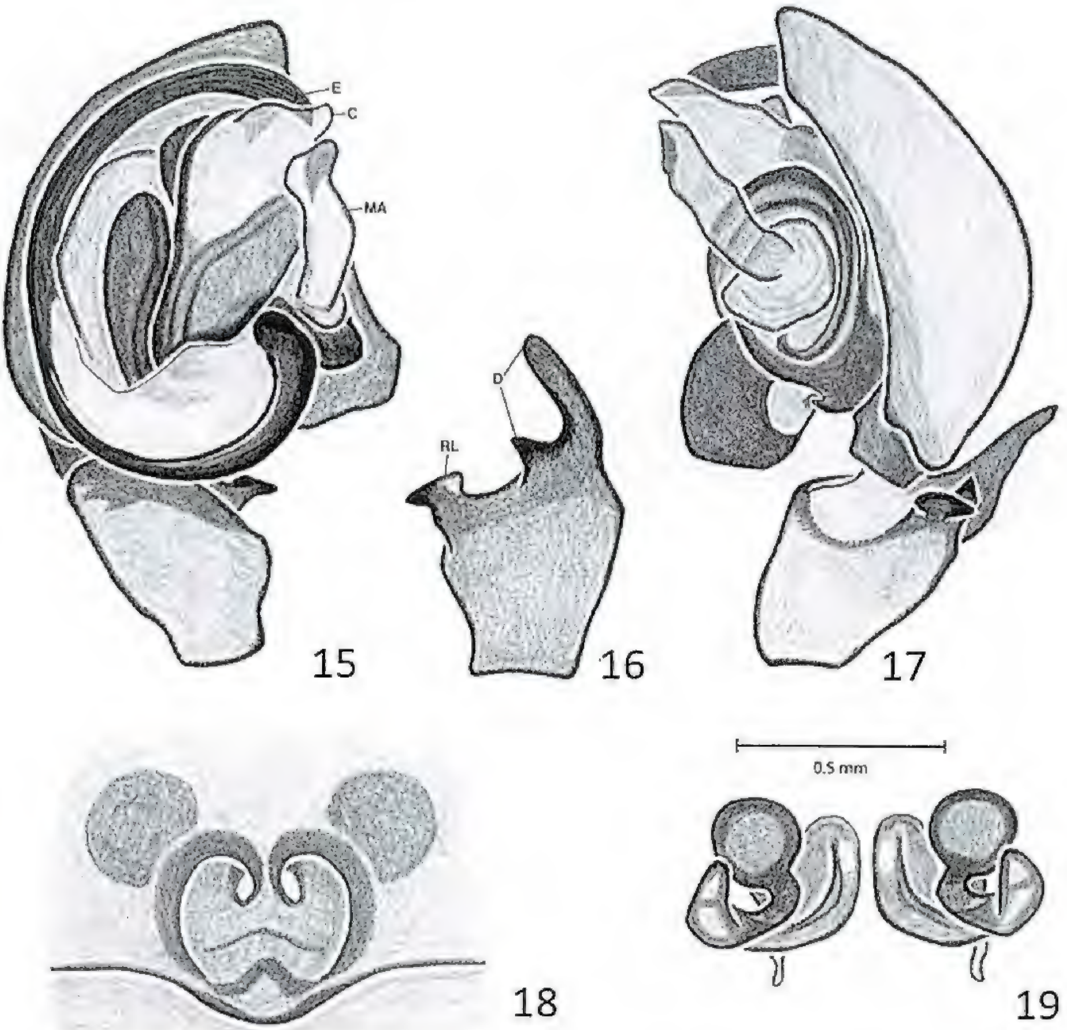
FIGURES 1–61



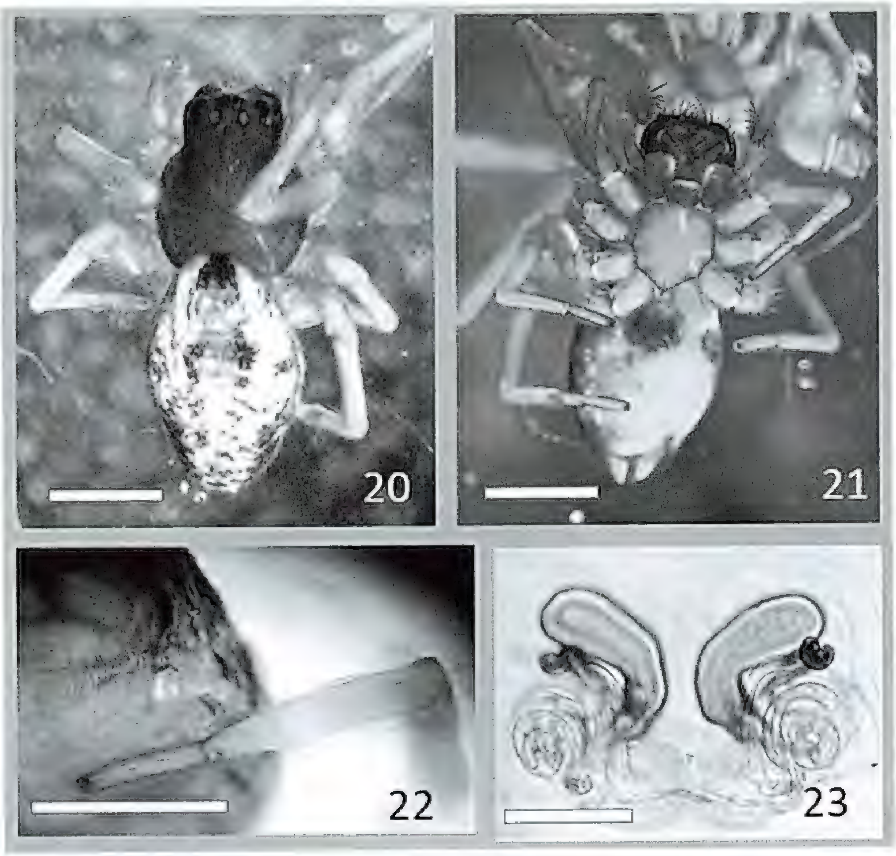
FIGURES 1–11. *Vytfutia labalaba* new species, Mt. Kinabalu, Borneo, CASENT9023842, female, morphology photos. 1. Cephalothorax, anterior, showing chelicerae and palps. 2. PME, dorsal, showing canoe-shaped tapeta. 3. ALE and PLE, lateral, showing canoe-shaped tapeta. 4. Cephalothorax, anterior, showing AER, clypeus and chilum. 5. Trochanter I. 6. Trochanter IV. 7. Posterior margin of carapace and pedicel, dorsal. 8. Left metatarsus IV, retrolateral, showing calamistrum. 9. Left palp, prolateral, arrows to probasal thorns. 10. Left leg I, prolateral. 11. Left leg IV, retrolateral. Scale bars, 1, 8, 9, 10, 11 = 0.5 mm, 2, 3, 4 = 0.25 mm, 5, 6, 7 = 0.1 mm.



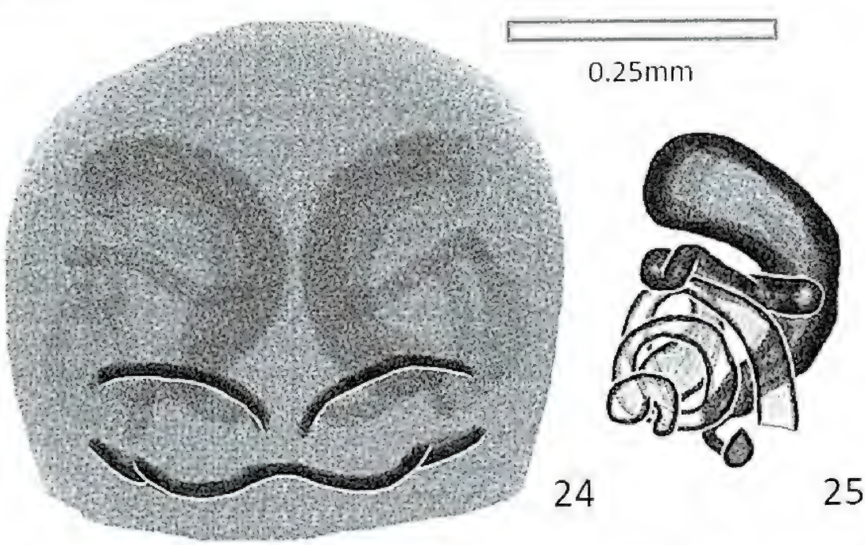
FIGURES 12–14. Spinnerets of female Phyxelididae. 12, 13. *Vytfutia labalaba* new species, Mt. Kinabalu, Borneo, CASENT9023842. 14. *Ambohima ranohira* Griswold, Wood and Carmichael, 2012, Ranohira, Madagascar, CASENT9019986. 12, 14. Ventral. 13. Lateral. Arrow and inset in 14 to stout, curved apicodorsal seta, which occurs in Phyxelidini and Vidoleini but not in Vytfutiini. Scale bar = 0.2 mm.



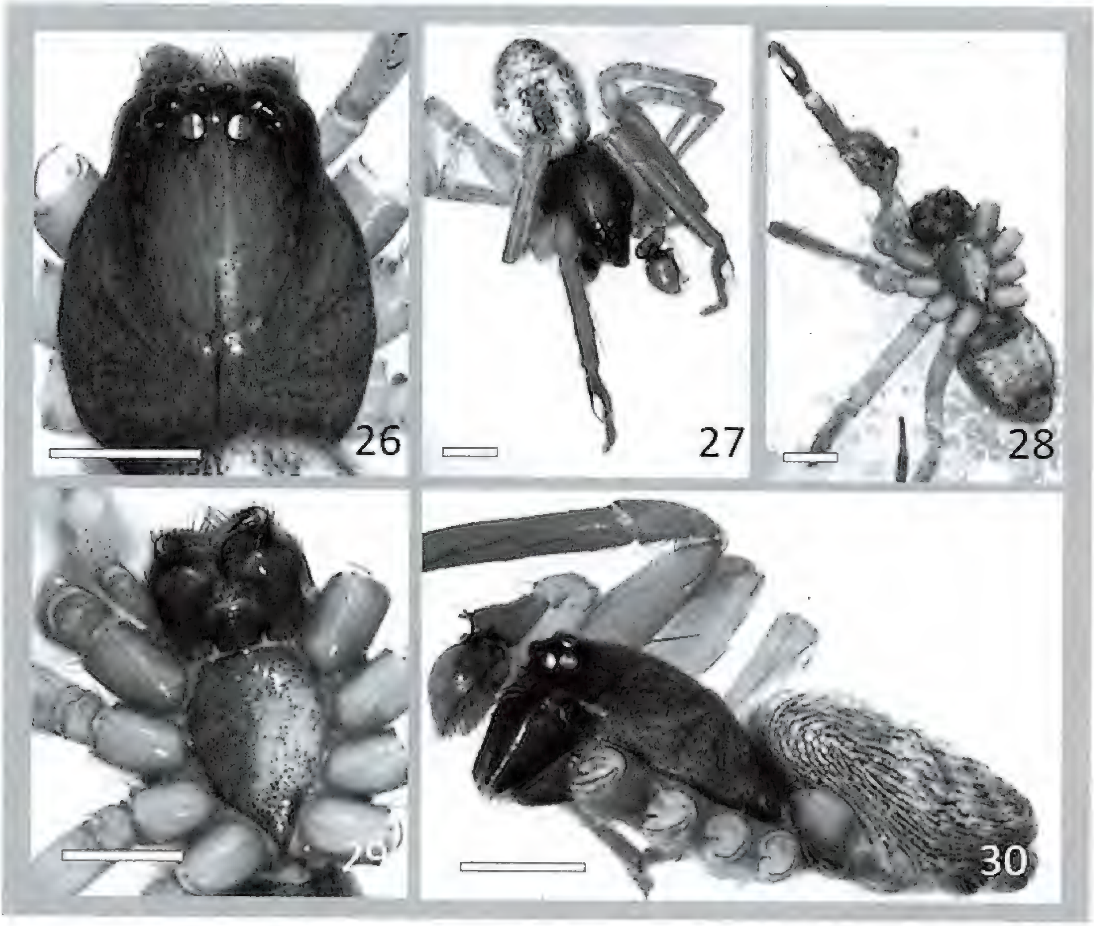
FIGURES 15–19. *Vytfutia bedel* Deeleman-Reinhold, 1986, genitalia-drawings, Holotype male and paratype female collected from Gunung Leuser, border of National Park at Bohorok in primary rainforest, N. Sumatra, Indonesia. 15–17. Male left palp. 15. Tibia and tarsus, ventral. 16. Tibia, dorsal. 17. Tibia and tarsus, retrolateral. 18, 19. Female genitalia. 18. Epigynum, ventral. 19. Vulva, dorsal. C = conductor; D = Dorsal tibial apophysis; E = embolus; MA = median apophysis; RL = retrolateral tibial apophysis.



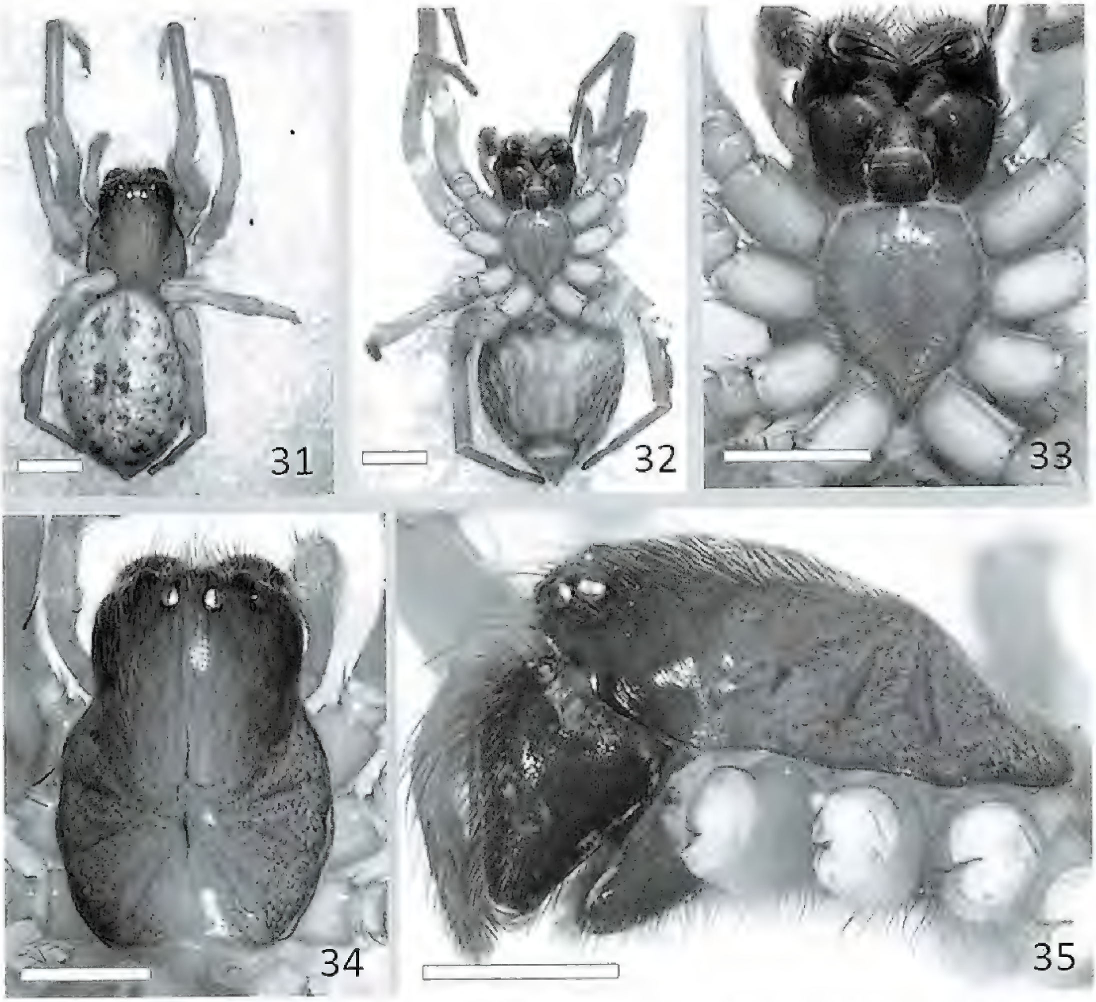
FIGURES 20–23. *Vytfutia halandrefana* new species, female, Berenty, Madagascar, CASENT9012513, habitus photos. 20. Dorsal. 21. Ventral. 22. Left metatarsus-tarsus IV and apex of abdomen with spinnerets, ventral. 23. Epigynal region, dorsal. Scale bars 20–22 = 0.5 mm, 23 = 0.25 mm.



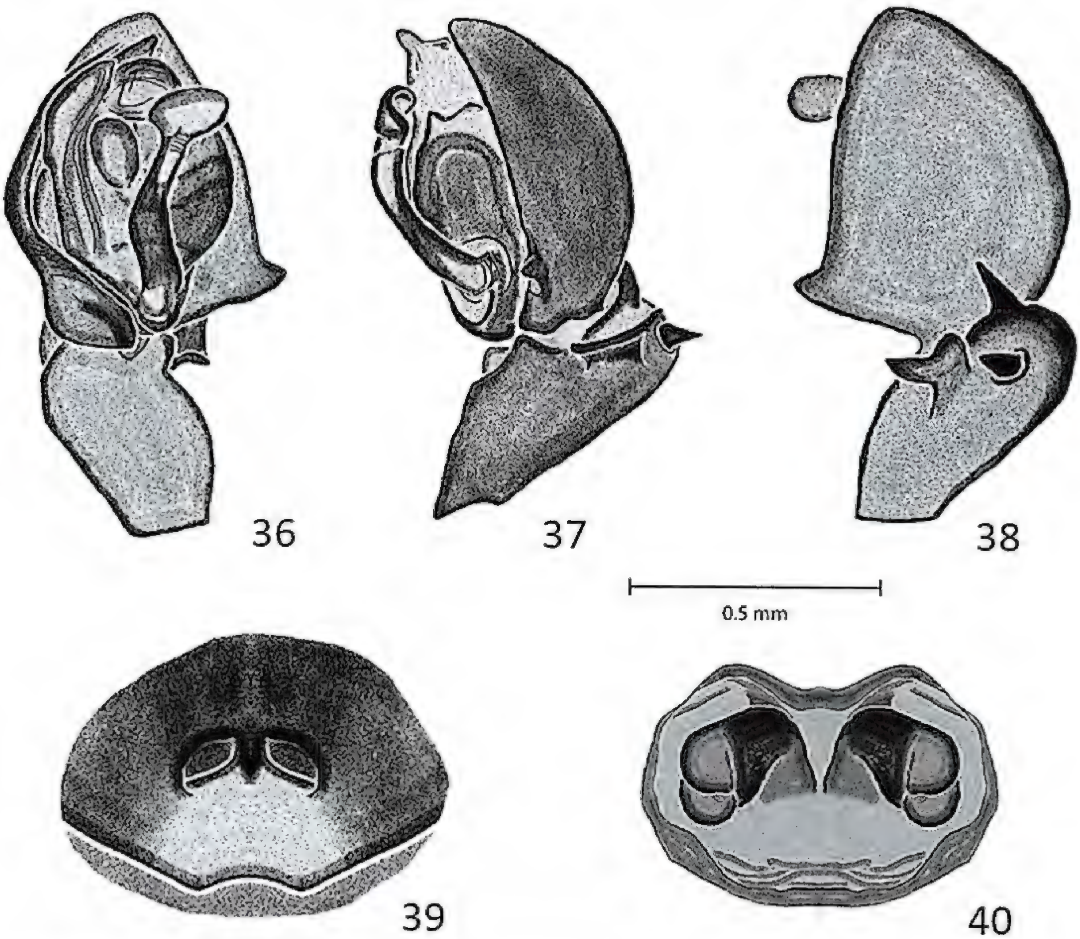
FIGURES 24, 25. *Vytfutia halandrefana* new species, female genitalia drawings, Tsingy de Bemaraha, Madagascar, CASENT9008848. 24. Epigynum, ventral. 25. Vulva, left half, dorsal.



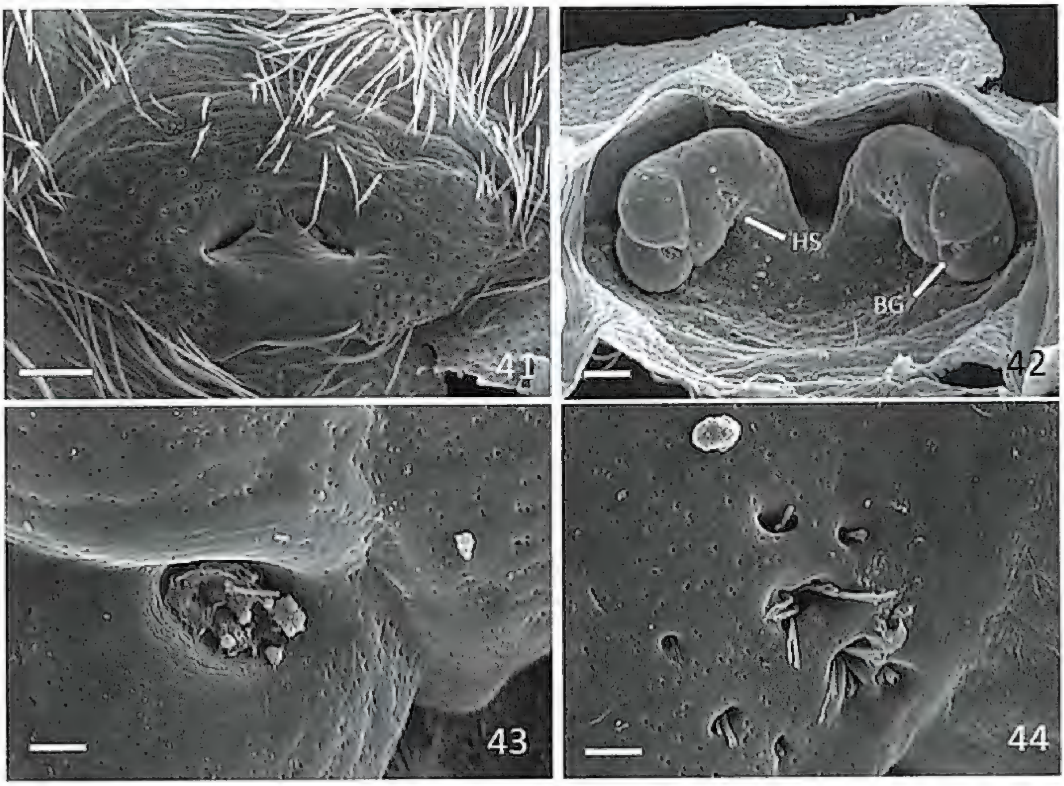
FIGURES 26–30. *Vytfutia labalaba* new species, Holotype male, Mt. Kinabalu, CASENT9023842, habitus photos. 26. Carapace, dorsal. 27. Dorsal. 28. Ventral. 29. Cephalothorax, ventral. 30. Lateral. Scale bar = 0.5 mm.



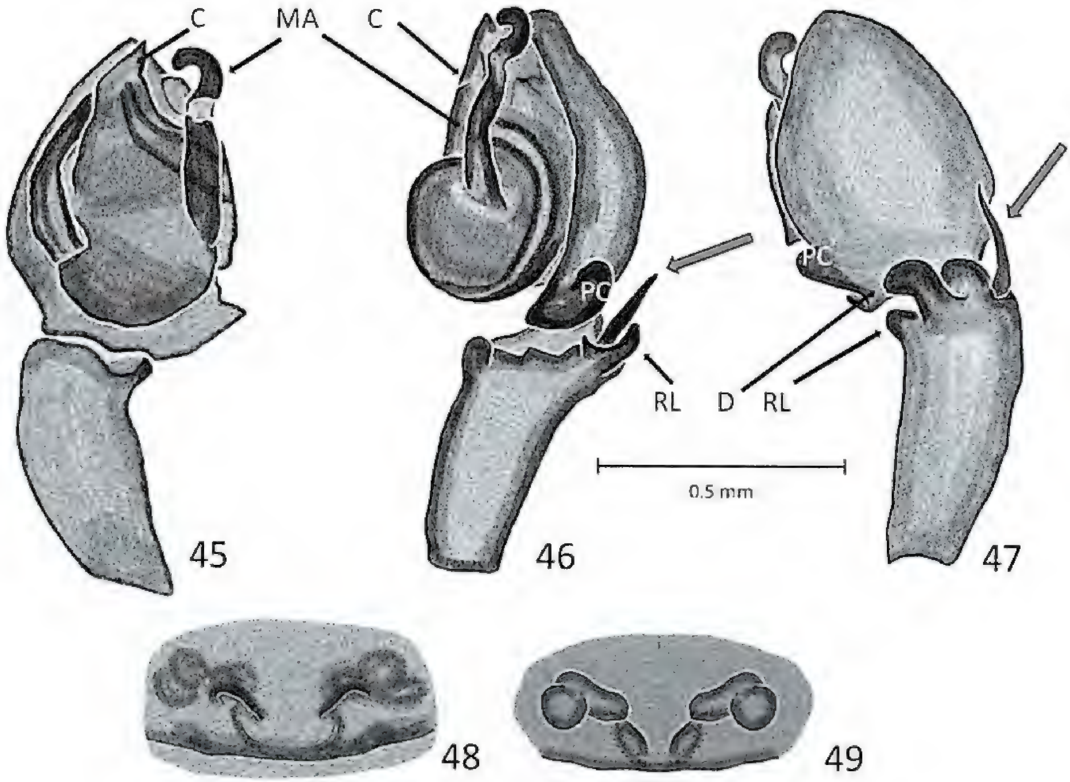
FIGURES 31–35. *Vytfutia labalaba* new species, Mt. Kinabalu, Borneo, CASENT9023842, female, habitus photos. 31. Dorsal. 32. Ventral. 33. Cephalothorax, ventral. 34. Cephalothorax, dorsal. 35. Cephalothorax, lateral. Scale bars = 0.5 mm.



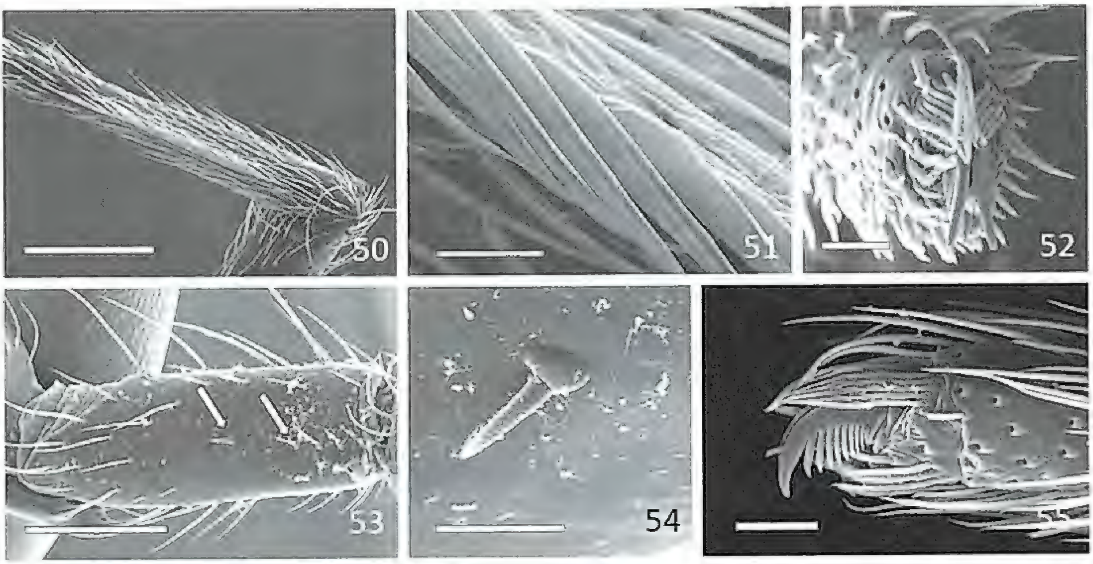
FIGURES 36–40. *Vytfutia labalaba* new species, genitalia-drawings. Holotype male and paratype female collected on the wall of a building at 1550 m elevation on Mt. Kinabalu, Sabah-Borneo, Malaysia, CASENT9023842. 36–38. Male left palp, tibia and tarsus. 36. Ventral. 37. Retrolateral. 38. Dorsal. 39, 40. Female genitalia. 39. Epigynum, ventral. 40. Vulva, dorsal.



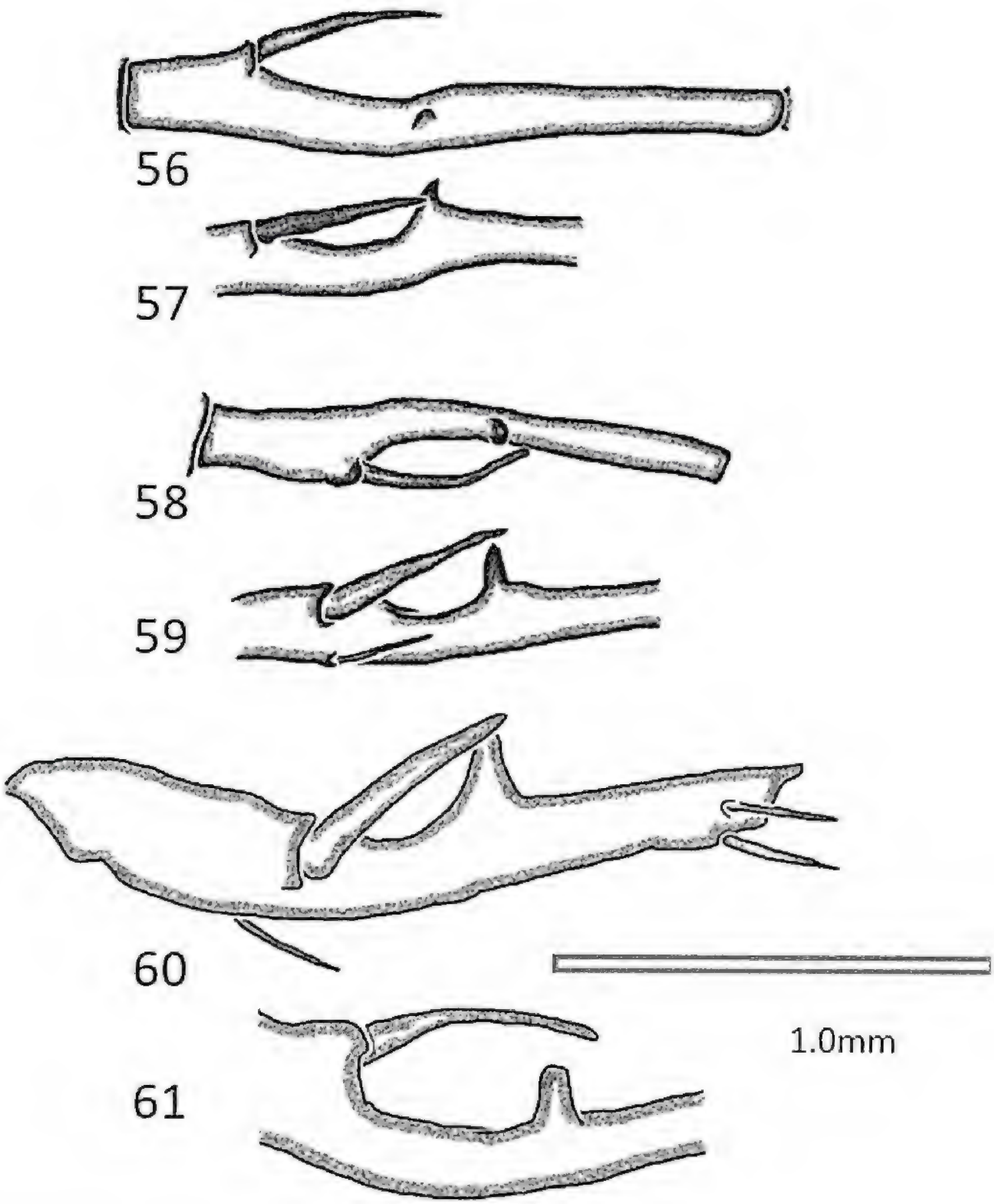
FIGURES 41–44. *Vytfutia labalaba* new species, Mt. Kinabalu, Borneo, CASENT9023842, female genitalia, scanning electron micrographs (SEM). 41. Epigynum, ventral. 42. Vulva, dorsal. 43. Bennet's gland pore (BG), left. 44. Pores of spermathecal head (HS), left. Scale bars, 41 = 100μm, 42 = 30μm, 43, 44 = 10μm.



FIGURES 45–49. *Vytfutia pallens* Deeleman-Reinhold, 1989, genitalia-drawings, male and female paratypes from Niah Cave, Sarawak, Malaysia. 45–47. Male left palp, tibia and tarsus. 45. Ventral. 46. Retrolateral. 47. Dorsal. 48. 49. Female genitalia. 48. Epigynum, ventral. 49. Vulva, dorsal. C: conductor, D: dorsal tibial apophysis, MA: median apophysis, PC: paracymbium, RL: retrolateral lobe of tibial apex. Grey arrow to tibial apical spine.



FIGURES 50–55. *Vytfutia halandrefana* new species, Berenty, CASENT9012420, female legs and palps, SEM. 50. Metatarsus IV, retrolateral, showing calamistrum. 51. Metatarsus IV, retrolateral, showing calamistral setae. 52. Tarsus IV, apical, showing STC and ITC. 53. Palpal femur, anterolateral, showing thorns (arrow). 54. Palpal femur, anterolateral thorn, close up. 55. Tarsus IV, retrolateral showing STC and ITC. Scale bars: 50, 300 μm; 51, 20 μm, 52, 55, 50 μm, 53, 200 μm, 54, 30 μm.



FIGURES 56–61. *Vytfutia* spp., male leg I with clasping modification of metatarsus. 56, 58, 61. Dorsal. 57, 59, 60. Retrolateral. 56, 57. *Vytfutia bedel* Deeleman-Reinhold, 1986, Holotype male from Gunung Leuser, border of National Park at Bohorok in primary rainforest, N. Sumatra, Indonesia, left. 58, 59. *Vytfutia labalaba* new species, Holotype male from the wall of a building at 1550m elevation on Mt. Kinabalu, Sabah-Borneo, Malaysia, CASENT9023842, right. 60, 61. *Vytfutia pallens* Deeleman-Reinhold, 1989, male paratype from Niah Cave, Sarawak, Malaysia, right. Scale bar = 1mm.

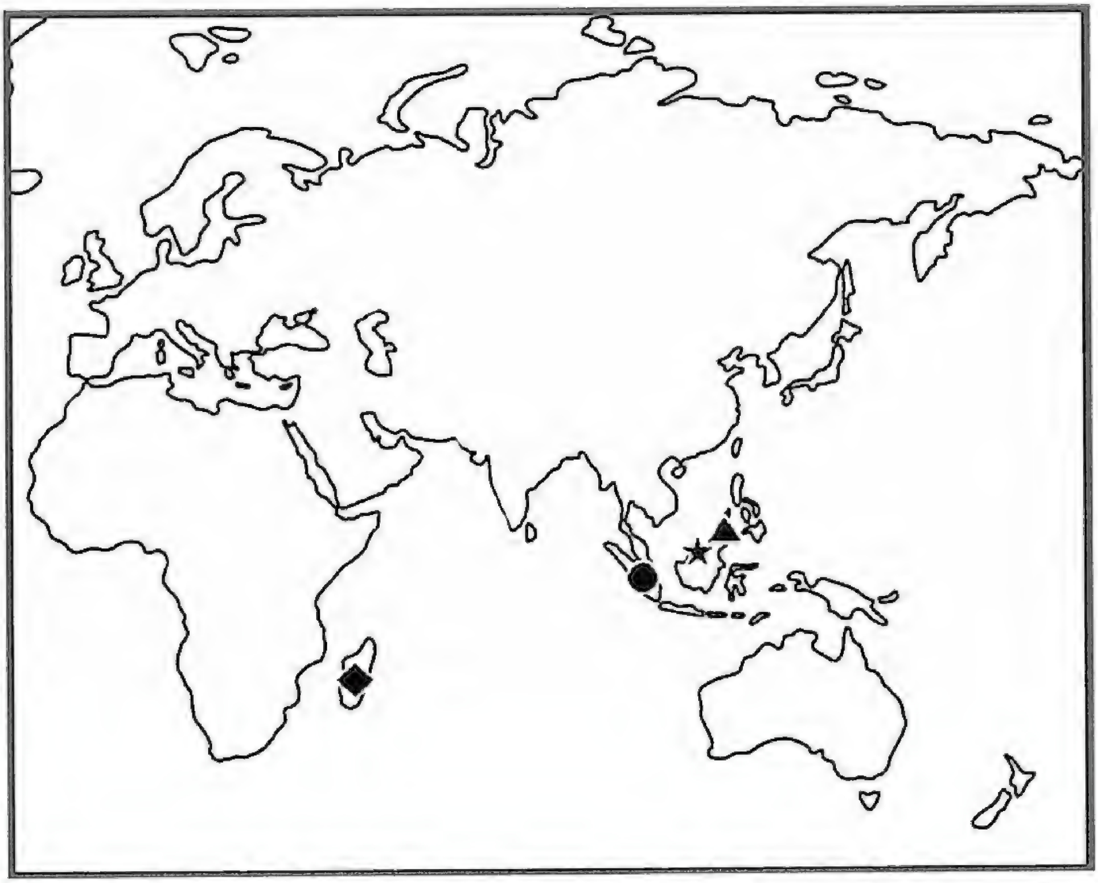


FIGURE 62. *Vytfutia* spp. Distributions on map of Eurasia and Australasia. Filled circle. *Vytfutia bedel* Deeleman-Reinhold, 1986, Holotype male from Gunung Leuser, border of National Park at Bohorok in primary rainforest, N. Sumatra, Indonesia. Triangle. *Vytfutia labalaba* new species, Holotype male from the wall of a building at 1550m elevation on Mt. Kinabalu, Sabah-Borneo, Malaysia. Diamond. *Vytfutia halandrefana* new species, Madagascar. Star. Vytfutia pallens Deeleman-Reinhold, 1989, male paratype from Niah Cave, Sarawak, Malaysia.

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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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A New Synonymy in Eurasian Crabronidae (Hymenoptera): *Lestica clypeata* (Schreber, 1759) and *Lestica quadriceps* (Bingham, 1897)

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Lestica quadriceps **(Bingham, 1897) from northern India is newly synonymized with a common Palearctic species** ***Lestica clypeata*** **(Schreber, 1759), based on a detailed comparison of their diagnostic characters.**

Bingham (1897) described *Crabro quadriceps* from a single female collected in the administrative division of Kumaun of India, now in the State of Uttarakhand. R. Turner (1912) synonymized this name with *Crabro alatus* Panzer (now in *Lestica*), but Leclercq (1950), who examined the holotype and who transferred the species to *Lestica*, proved this synonymy wrong. As he pointed out, the pygidial plate in the female of *L. quadriceps* is scooplike and conspicuously narrowed in the distal half (Fig. 3), whereas it is flat and relatively broad in *L. alata*. In 1958, he included *L. quadriceps* in his key to the subgenus *Solenius* of southeast Asia, thus providing additional recognition characters for the species. Saini and Dey (2021) redescribed the female and described the male, including topotypical specimens of both sexes from Khanabal in Jammu and Kashmir, and their paper allows an even better understanding of the species.

An analysis of Leclercq's 1958 key and of Saini and Dey's description clearly demonstrates that *L. quadriceps* is morphologically identical with *L. clypeata* (Schreber), **new synonymy**, and is nothing more than a higher elevation Indian population of that species. No significant differences exist between them. The females of both share the following recognition features: clypeal middle carina convex dorsally (Fig. 1), curved in profile (Fig. 2), projecting ventrally into narrow, apically emarginate middle lobe; free margin of clypeus with tooth on each side of lobe (Fig. 1); pronotum with anterolateral denticle (Fig. 3); mesothoracic venter, on each side of middle carina, coarsely punctate, with linear interspaces (Fig. 4); tibiae all yellow; pygidial plate scooplike, conspicuously narrowed in distal half, with long, dense setae on each side (Fig. 5). The males can be instantly recognized by the following leg modifications: forebasitarsus (Fig. 8) greatly expanded (width slightly greater than length), foretarsomeres II-IV wider than long but markedly narrower than I (Fig. 8), midfemur spinose basally (Fig. 9), and hindtrochanter spinose (Fig. 10). Subsidiary recognition features are: head markedly narrowed behind eyes (Fig. 6), mandible bidentate apically, flagellomere I 1.5–2.0 × as long as wide, apical flagellomere

almost straight, pronotum lateral margins converging anteriorly (Fig. 7), foretrochanter carinate ventrally, forefemoral venter carinate throughout, midtrochanter obtusely angulate ventrally, midfemoral venter carinate throughout.

DISTRIBUTION.— England to Russian Far East, in Europe north to Scandinavia, Finland, and lakes Ladoga and Onega areas in Russia, in Kazakhstan only in southeastern mountains, Kyrgyzstan and Uzbekistan, North Africa (northeastern Egypt, Tunisia, Algeria, Morocco), Turkey, Israel, Iran, Iraq, Syria, northern India (states of Himachal Pradesh, Jammu and Kashmir, and Uttarakhand).

ACKNOWLEDGMENTS

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SAINI, V., and D. DEY. 2021. Contribution to the knowledge of little known Crabronid wasps (Hymenoptera: Crabronini) of India. *Journal of Entomological Research* 45 (Supplement):1074-1079.

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ILLUSTRATIONS

Figures 1–10

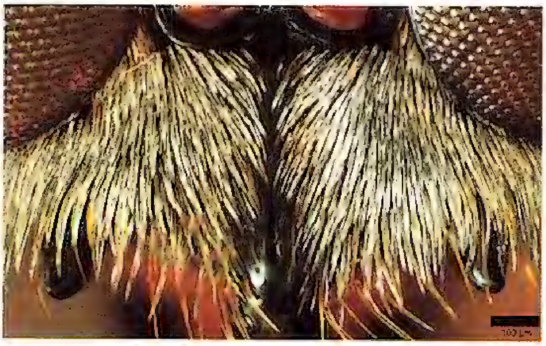

FIGURE 1. Female clypeus in front view.

FIGURE 2. Female clypeus in lateral view.

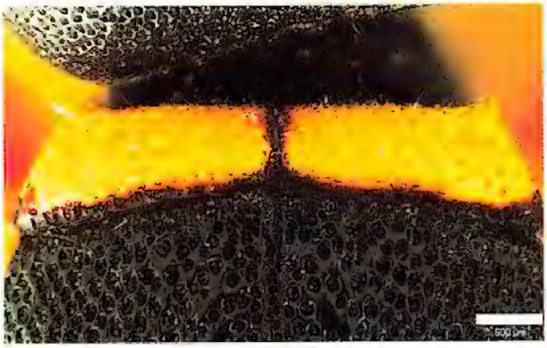

FIGURE 3. Female pronotum.

FIGURE 4. Mesothoracic venter of female.

FIGURE 5. Female pygidial plate.

FIGURE 6. Male head in dorsal view.

FIGURE 7. Male pronotum in dorsal view.

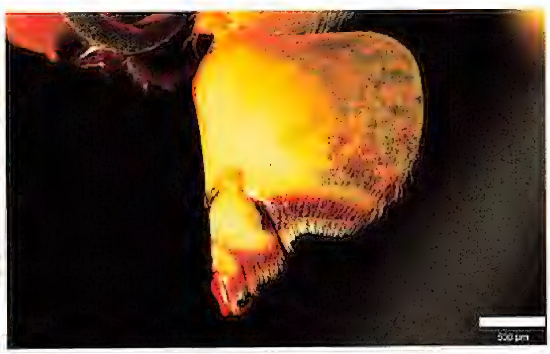

FIGURE 8. Male foretarsus.

FIGURE 9. Base of male midfemur.

FIGURE 10. Male hindtrochanter.

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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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A Revision of the Genus *Paranysson* Guérin-Méneville, 1844 (Hymenoptera: Crabronidae)

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The genus *Paranysson* is revised, its species are redescribed, taxonomically important characters illustrated, and the collecting localities mapped. The known ranges of species are greatly extended. The previously unknown male of *Paranysson inermis* is described. An original key for species identification is provided, including several previously unobserved characters. The following are new synonyms: *Pseudoheliorycies foxii* Ashmead, 1899 = *Paranysson abdominalis* (Guérin-Méneville, 1844), and *Paranysson bumbanus* Leclercq, 1968 = *Paranysson helioryctoides* (R. Turner, 1912).

Paranysson, a well-defined genus of Miscophini, comprises eight species. Seven occur in sub-Saharan Africa and one is Oriental (also recorded from the southern tip of the Arabian Peninsula). The genus was described in 1844, but was not properly understood until R. Turner's work of 1914, when it was solidly defined. This revision establishes two new synonymies, recognizes the male of *Paranysson inermis,* presents an updated key for species identification, greatly extends the known species ranges, and adds a number of previously unnoted recognition characters, some of them of primary importance.

Methods and Technical Terms. The specimens were examined under a Leica MZ APO stereomicroscope with a fluorescent light illuminator. The illustrations were taken through the Automontage software package by Syncroscopy, except two were taken under a Scanning Electron Microscope. Distribution maps were generated using ArcMap, version 10.5 program. Molecular techniques have not been attempted as the goal of this revision is species identity and recognition.

In the Species Descriptions section, species are arranged alphabetically. Most of the morphological characters are as in Bohart and Menke (1976), but my terms for the clypeus need a clarification:

- **basal part** is densely punctate and covers most of the clypeal surface;
- **bevel** is the shiny, impunctate or sparsely punctate medioventral part, separated from the free margin by a lamella;
- **lamella** is the ventral, narrow part of the clypeus, separated from the bevel by an angle or sulcus, also impunctate, and extending along the entire margin of the median lobe; although ill-defined in some species;
- **median lobe** is the medioventral, prominent part of the clypeus;
- **lateral lobe** is the ventral, not prominent section of the clypeus on each side of the median lobe.

Origin of Material. The specimens examined (a total of 732) or otherwise mentioned in the text, are deposited in the institutions listed below. The institutions are referred to by their respec-

tive capitalized abbreviations that precede their full names in the list below (the name of the person responsible for sending specimens is given in parentheses):

AMNH: American Museum of Natural History, New York, New York, USA (Christine Lebeau).
ANSP: Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, USA (Jason D. Weintraub).
BMNH: The Natural History Museum (formerly British Museum (Natural History)), London, United Kingdom (Joseph Monks).
CAS: California Academy of Sciences, San Francisco, California, USA.
MRAC: Musée Royal de l'Afrique Centrale, Tervuren, Belgium (Stéphane Hanot).
MSNG: Museo Civico di Storia Naturale di Genova, Genova, Italy.
OÖLM: Oberösterreichisches Landesmuseum, Linz, Austria (Esther Ockermüller).
SAM: South African Museum, Iziko Museum of Cape Town, Cape Town, South Africa (Simon van Noort, Aisha Mayekiso).
TMP: The Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria, South Africa.
UCD: R.M. Bohart Museum of Entomology, University of California Davis, Davis, California, USA (Steven L. Heydon).
USNM: United States National Museum, Smithsonian Institution, Washington, D.C. (Seán Brady).

Genus *Paranysson*

Paranysson Guérin-Méneville, 1844:441 (as subgenus of *Nysson*). Type species: *Nysson abdominalis* Guérin-Méneville, 1844, by monotypy.
Helioryctes F. Smith, 1856:358. Type species: *Helioryctes melanopyrus* F. Smith, 1856, by monotypy.
Pseudohelioryctes Ashmead, 1899:248. Type species: *Pseudohelioryctes foxii* Ashmead, 1899, by original designation and monotypy.

RECOGNITION. The following characters place *Paranysson* within the tribe Miscophini: posterior mandibular margin notched; ocelli round and convex; inner eye margins not emarginate, converging above; antennal socket contiguous with frontoclypeal suture; clypeus not divided by vertical sutures into three parts; anal lobe of hindwing at most as long as half submedial cell; hindfemur thickest near middle, with apex simple.

Within Miscophini, the genus shares the presence of three submarginal cells, the second being petiolate, with *Plenoculus*, *Solierella*, and *Sphodrotes*. It differs from all three in having an emarginate lateral margin of female tergum V (Fig. 1), a previously unnoticed character that differentiates *Paranysson* from all other Larrinae, and in having the penis valves fused and unusually broadened in apical half, truncate apically (Figs. 43, 50). In addition, *Solierella* differs from *Paranysson* by a number of characters (see Bohart and Menke,

FIGURE 1. *Paranysson abdominalis* (Guérin-Méneville). Gastral apex of female (arrow shows lateral emargination of tergum V).

1976:294), and the Australian genus *Sphodrotes* in having the occipital carina effaced before reaching the hypostomal carina, the propodeal enclosure setose (setae at least fine, inconspicuous), sternum I with a posteromedian prominence, and the pygidial plate absent in both sexes. In *Paranysson*, the occipital carina joins the hypostomal carina just before the latter's apex, the propodeal enclosure is asetose, sternum I has no apicomedian prominence, and the pygidial plate is present in both females and males. The closest to *Paranysson* is *Plenoculus*. In the latter genus, however, the propodeal dorsum is finely granulate or finely ridged and the occipital carina is incomplete below (Bohart and Menke, 1976:294). In *Paranysson* the propodeal dorsum is areolate or reticulate, and the occipital carina meets the hypostomal carina (other differences given by these authors separate only some, but not all *Paranysson*).

Male genitalia are nearly identical in most species (Fig. 50), except that in *P. oscari* the apical part of penis valve has a spine-like lateral process (Fig. 43).

According to Lomholdt (1985), *Paranysson* shares with *Plenoculus* the gonocoxite (as gonostyle) constricted subapically, and penis valves coalesced and expanded apically. This statement is poorly substantiated: in some *Plenoculus*, e.g., *P. cockerellii* W. Fox, and *P. palmarum* F. Williams, the gonocoxite is not constricted subapically (see Figs.70-72 in Williams, 1960), and at least in *P. propinquus* W. Fox the penis valves are not expanded apically and not coalesced (Fig. 82 of Williams, 1960).

Taxonomic History. Guérin-Méneville (1844) described *Paranysson* from Senegal as a subgenus of *Nysson*, as reflected in its name, obviously because of the petiolate second submarginal cell shared by both. He included only one species, *Nysson abdominalis*, which thus became the type species of *Paranysson* by monotypy. F. Smith (1856) was aware of Guérin-Méneville's description, but did not recognize his species and described a closely related *melanopyrus* in the new genus *Helioryctes*. A big confusion followed. Cresson (1882) and Schrottky (1910) described in *Paranysson* two North American and two Argentinian species, respectively, which are now known to be *Zanysson* and *Metanysson* (Handlirsch, 1887 reported Cresson's species in the subgenus *Paranysson* of *Nysson*). Ashmead, (1899) believed that his new species *foxii* from Ethiopia was a female differing from *Helioryctes* by the absence of a hindcoxal spine or tubercle and thus deserving a new generic name, *Pseudohelioryctes*; the unarmed hindcoxa, however, is due to the fact that the specimen is a male (and a junior synonym of *Paranysson abdominalis*). In the same paper Cresson transferred from *Nysson* to *Paranysson* three North American species (for a total of five), now classified as *Zanysson*. Handlirsch (1887), Fox (1894), Kohl (1897), and Ashmead (1899) treated *abdominalis* as a *Nysson* (subfamily Nyssoninae, now Bembicinae) because they knew it only through the original description. Kohl (1897) and Ashmead (1899), however, recognized the synonymic names *Helioryctes* and *Pseudohelioryctes*, respectively, as members of Larrinae. Bingham (1897) transferred *Paranysson abdominalis* to *Helioryctes*, assuming the identity of the two genera, but incorrectly used as valid the younger name *Helioryctes*. R. Turner synonymized *Helioryctes* with *Paranysson* in 1912, and *Pseudohelioryctes* with *Paranysson* in 1914. Since then, only *Paranysson* has been used for the genus in the subsequent literature, and no nyssonine has been described in (or transferred to) it.

Kohl (1897:397) thought that *Paranysson* was just a *Nysson* with somewhat more developed hindtibial spines. He also thought (1897:388) that *Helioryctes* (that he knew only through the original description) closely resembled the Australian *Sericophorus*, whereas Dalla Torre (1897) placed these two genera (and also *Sphodrotes*) in the new subfamily Sericophorinae. Turner (1914) accepted this concept, but renamed the subfamily Paranyssoninae (correctly: Paranyssontinae), wrongly thinking that "as *Paranysson* is an older name than *Sericophorus*, it should be used for the subfamily". Modern researchers (Leclercq, 1968; Bohart and Menke, 1976) observed the morpho-

logical similarity between Sericophorinae and Miscophini and combined them into one tribe. Bohart and Menke (1976) provided a detailed description of the genus.

R. Turner (1914) was also the first author to review the six species of *Paranysson* described by that time by Guérin-Méneville, 1844, F. Smith, 1856, Bingham, 1897, Ashmead, 1899, Cameron, 1910, and by himself in 1912, describing in 1914 another new species, and generating a key for the identification of females (the poorly described *P. foxii* was excluded). Arnold (1923), in his monograph of southern African Sphecidae, dealt with *Paranysson*, but his key is no more than a slight modification of Turner's; in particular, he did not add any new characters. Leclercq (1968), on the other hand, greatly expanded his key, providing a number of previously unused characters, and also including the males and describing two new species (one of which is a junior synonym). He had, however, not seen three species (*P. abdominalis*, *P. foxii*, *P. helioryctoides*), and relied on existing descriptions for their characteristics. Some of his characters (e.g., sculpture of the propodeal dorsum, lateral propodeal carina with or without tooth) are variable and do not guarantee a correct identification.

Overall, the papers by the three authors suffered from the following: 1. *P. foxii* was known to them only through the insufficient original description, 2. the male of *P. helioryctoides* remained unknown, and 3. populations of *P. abdominalis* with an all-black thorax were not recognized. The authors also missed some excellent diagnostic features such as the structure of the clypeus, the impunctate mandibular base in *P. oscari*, and the shape of flagellomere I in the male of *P. abdominalis*.

Nesting Behavior. Arnold (1923:13) first noticed that *Paranysson* nest in sandy soil and that "*P. quadridentatus* has a most powerful odor of bugs". Subsequently Bequaert (1933) observed the nesting habits of *P. melanopyrus* at Kasenga, Haut-Katanga Province of the Democratic Republic of the Congo. Each nest he studied consisted of a nearly straight, vertical gallery, 6-8 mm wide, sunk in the bare sand to a depth of about 75 cm. The lower end of the gallery branched into a few more or less horizontal cells, placed at about the same level in various directions. Each cell was 10-12 mm long and 4-5 mm in diameter. At the nest entrance there was a mound of loose sand, about 12 cm long, 9 cm wide, and 3 cm high. A curved tunnel ran through the longitudinal axis of the mound; it was slightly wider than the gallery to which it led, and opened at the narrow end of the mound. The sand was more closely packed together and apparently cemented, either by moisture or by saliva, about the tunnel.

The prey found in the cell consisted of various instar larvae of the pentatomid *Natalicola pallidus* (Westwood), usually six or seven per cell.

While collecting *Paranysson* in various African countries, I also noticed this strong odor. Obviously, the source is the pentatomid prey.

Cladistic Analysis

The following is the list of characters used in the analysis below:

Occipital carina: 0. meeting hypostomal carina, 1. not meeting hypostomal carina.
Male palpi: 0. not unusually setose, 1. conspicuously setose.
Length of apical flagellomere: 0. no more than 2.2 × basal width, 1. equal to 2.6 × basal width.
Male flagellomere I: 0. not or minimally concave ventrally, 1. concave ventrally.
Wing membrane: 0. translucent or nearly so, 1. conspicuously infumate.
Propodeal enclosure: 0. setose, 1. asetose
Propodeal enclosure: 0. unsculptured between ridges, 1. finely granulose between ridges.

Lateral carina of propodeum: 0. absent, 1. present, in most specimens broadened posteriorly, 2. forming a spine posteriorly in all or most specimens.
Female hindcoxa: 0. simple, 1. with tubercle in at least some specimens, 2. with conspicuous spine.
Lateral margin of female tergum V: 0. straight. 1. emarginate.
Male tergum VI: 0. closely punctate, 1. sparsely punctate
Male tergum VI: 0. without lateral carina, 1. with obtuse, lateral carina.
Female pygidial plate: 0. present, 1. absent
Male pygidial plate: 0. absent, 1. present but ill defined, 2. well defined, broad, 3. well defined, narrow, triangular.

Sphodrotes punctuosa Kohl *and Plenoculus davisi* W. Fox, the type species of these two genera, respectively, were used as the outgroup, and the following data matrix was constructed:

Sphodrotes punctuosa	10000 00200 0010
Plenoculus davisi	10000 11000 0001
Paranysson abdominalis	00011 10121 0002
Paranysson assimilis	00000 10211 0002
Paranysson brevispinosus	00001 10221 0002
Paranysson helioryctoides	00001 10211 0002
Paranysson inermis	00101 10001 1103
Paranysson melanopyrus	00001 10221 0002
Paranysson oscari	01001 10021 1102
Paranysson quadridentatus	00001 10121 0002

A cladistic analysis was kindly performed by Fernando Álvarez Padilla of the Universidad Nacional Autónoma de México through implicit enumeration, using T.N.T. program by Pablo Goloboff, Steve Farris, and Kevin Nixon (2003). Three equally parsimonious trees were found, and the strict consensus tree is represented in Fig. 2. The strict consensus tree has mapped only the synapomorphies common to all cladograms and the root is collapsed to be represented correctly.

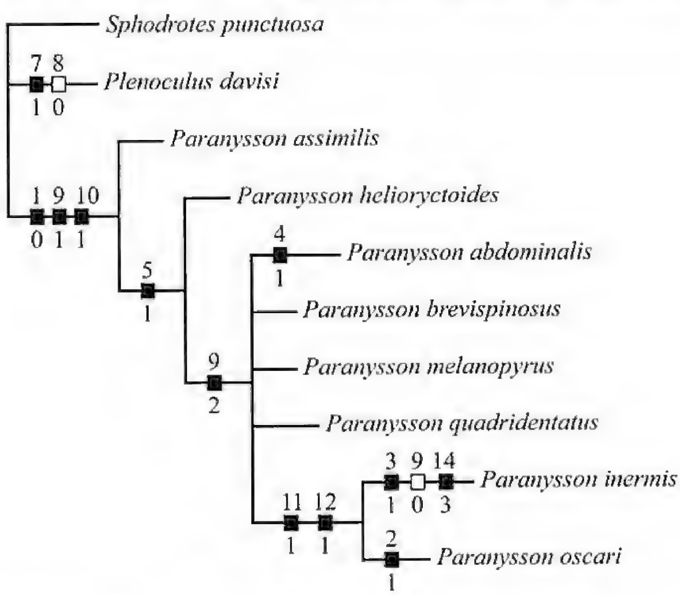


FIGURE 2. Phylogenetic tree of *Paranysson*.

Key to species of *Paranysson*

1. Wing membrane nearly hyaline (Fig. 11); femora black; ocellocular distance 0.30-0.35 × distance between hindocelli (Fig. 12); length no more than 7.0 mm. Oriental, also recorded from southern tip of Arabian Peninsula . . . . *P. assimilis* Bingham
- Wing membrane conspicuously infumate (Fig. 3) except slightly so in some *P. helioryctoides*; mid- and hindfemora in vast majority of specimens ferruginous; ocellocular distance 0.40-1.20 × distance between hindocelli; length in most specimens more than 7.0 mm. Africa south of Sahara. 2

2. Basal portion of mandible impunctate or with only a few, sparse punctures (Fig. 39); clypeal bevel in most specimens markedly inclined between basal part and lamella (Figs. 37, 38), perpendicularly so in some females. Female: hindcoxal spine robust, with appressed setae ventrally, originating closer to anterior margin than to posterior (Fig. 40). Male: palpi conspicuously setose (Fig. 41). . . . . *P. oscari* (R. Turner)
- Basal portion of mandible finely, closely punctate; clypeal bevel not markedly inclined toward basal clypeal part. Female: hindcoxal spine, when present, thin, asetose ventrally, and originating at hindcoxa midlength or closer to posterior margin than to anterior. Male: palpi usual, not conspicuously setose. 3

3. Length of apical flagellomere 2.6 × its basal width (Fig. 30); propodeum without carina between lateral and posterior surfaces (Fig. 28). Female: clypeal free margin without lateral teeth (Fig. 26); hindcoxa unarmed, without tubercle or spine (Fig. 29). Male: terga III-VII to V-VII sparsely punctate; tergum VI with obtuse lateral carina (Fig. 31); pygidial plate narrow, triangular (Fig. 31). . . . . *P. inermis* Leclercq
- Length of apical flagellomere at most 2.2 × its basal width; propodeum with longitudinal carina between lateral and posterior surfaces, carina projecting as triangular tooth at about two thirds of length or broadened there (Fig. 6), exceptionally not broadened. Female: clypeal free margin with lateral teeth (except teeth absent or ill-defined in *P. helioryctoides*); hindcoxa either with spine or acute tubercle (Figs. 6, 19, 24, 35, 40, 47). Male: terga III-VII closely punctate; tergum VI without obtuse lateral carina, pygidial plate broad, not triangular.. . . . 4

4. Females. 5
- Males. 9

5. Clypeal bevel separated by carina from basal part (Fig. 22); hindcoxal venter with acute tubercle but without spine (Fig. 24). . . . . *P. helioryctoides* R. Turner
- Clypeus without carina between bevel and basal part; hindcoxal venter with conspicuous spine. 6

6. Hindcoxal spine originating next to apical coxal margin (Fig. 19); lateral clypeal teeth protruding beyond free clypeal margin between them (Fig. 17). . . . . . . *P. brevispinosus* Arnold
- Hindcoxal spine originating at least half midocellar diameter before apical coxal margin (Figs. 7, 35, 47); lateral clypeal teeth not protruding beyond free clypeal margin between them (Figs. 4, 33, 45). 7

7. Dorsal length of flagellomere I 1.4-1.6 × apical width; hindcoxal spine originating at or before

hindcoxal midlength (Fig. 35); longitudinal carina between propodeal side and posterior surface in most specimens forming sharp tooth at about two thirds of length. . . . . *P. melanopyrus* (F. Smith)

- Dorsal length of flagellomere I 2.0-2.4 × apical width; hindcoxal spine originating next to hindcoxal apex, on its inner side; longitudinal carina between propodeal side and posterior surface slightly broadened at about two thirds of length, but in most specimens not forming sharp tooth. 8

8. Hindcoxal spine as long as hindcoxal venter or longer (Fig. 47); pygidial plate finely, sparsely punctate throughout (Fig. 48); thorax and propodeum all black. . . . . *P. quadridentatus* (Cameron)

- Hindcoxal spine shorter than hindcoxal venter (Fig. 7); pygidial plate rugose except basally (Fig. 8); pronotum, scutellum posteriorly, and postscutellum ferruginous in specimens from Senegal, Mali, and Niger (Fig. 3), in some specimens also propodeal enclosure, but all black in those from Ethiopia, Kenya, and Tanzania. . . . . *P. abdominalis* (Guérin-Méneville)

9. Tergum II impunctate basomedially or with a few sparse punctures (Fig. 20); hindcoxal venter in large specimens with apical tooth on inner side. . . . . *P. brevispinosus* Arnold

- Tergum II closely punctate throughout; hindcoxa without apical tooth. 10

10. Flagellomere I concave ventrally (Fig. 9); ocellocular distance equal to distance between hindocelli or slightly greater; pronotum, scutellum posteriorly, postscutellum, and often part of mesopleuron and propodeal enclosure ferruginous in specimens from Senegal, Mali, and Niger (as in Fig. 3), but all black in those from Ethiopia, Kenya, and Tanzania. . . . . *P. abdominalis* (Guérin-Méneville)

- Flagellomere I slightly flattened ventrally, not or minimally concave; ocellocular distance smaller than distance between hindocelli; thorax and propodeum all black. 11

11. Free margin of clypeal lobe obtusely angulate laterally (Fig. 23). . . . . *P. helioryctoides* (R. Turner)

- Free margin of clypeal lobe different. 12

12. Clypeal lamella emarginate mesally, each side of emargination slightly protruding as obtuse tooth (Fig. 34), distance between teeth apices equal to 1.2-1.8 × midocellar diameter; dorsal length of flagellomere I equal to 1.0-1.2 × that of flagellomere II; hindcoxal venter without transverse, preapical carina, all punctate, not concave apically. . . *P. melanopyrus* (F. Smith)

- Clypeal free margin gently arcuate mesally, at most with pair of admedian rudimentary teeth (Fig. 46); dorsal length of flagellomere I equal to 1.2-1.6 × that of flagellomere II; hindcoxal venter with preapical, semicircular carina, concave and unsculptured between carina and apex (Fig. 49). . . . . *P. quadridentatus* (Cameron)

Species Descriptions

Paranysson abdominalis (Guérin-Méneville)

Figures 1, 3-10.

Nysson abdominalis Guérin-Méneville, 1844:441, ♀ (as *abdominale*, incorrect original termination). Syntypes: ♀, Senegal: no specific locality (MSNG), not examined. – F. Smith, 1856:355 (in catalog of Hymenoptera in British Museum); Gerstaecker, 1867:122 (comments based on original description); Handlirsch, 1887:318 (original description translated into German, discussion of generic relationships); de Dalla Torre, 1897:567 (in catalog of world Sphecidae); Bingham, 1902:212 (South Africa: Pretoria). – As ***Helioryctes abdominalis***: Bingham, 1897:271 (new combination, West Africa). – As ***Paranysson abdominalis***: R. Turner, 1914:340 (new combination, in revision of *Paranysson*); Arnold, 1923:14 (in revision of African *Paranysson*), 1930:7 (in checklist of Afrotropical Sphecidae, as *abdominale*); Guiglia, 1948:180 (type in Genova, Italy), 189 (redescription of type); Leclercq, 1968:84 (in revision of African *Paranysson*); R. Bohart and Menke, 1976:308 (in checklist of world Sphecidae).

As *Helioryctes melanopyrus*: W. Fox, 1896:554 (Ethiopia: Lake Stephanie, now Chew Bahir), corrected to *Pseudohelioryctes foxii* by Ashmead, 1899:248; Magretti, 1898:49 (Somalia), tentatively corrected to *Paranysson foxii* by Leclercq, 1968:85.

Pseudohelioryctes foxii Ashmead, 1899:248, ♀, correctly ♂ (as *Foxii*, incorrect original capitalization). Holotype: ♀, Ethiopia: near Lake Stephanie, now Chew Bahir (ANSP), examined [according to Pate (1937:55, subscript), the type is a male taken about six miles due north of Kulama at the north end of Lake Donaldson, an arm of Lake Stephanie]. **New synonym.** – As ***Paranysson foxii***: R. Turner, 1914:343 (new combination, original description copied); Leclercq, 1968:85 (in revision of African *Paranysson*); R. Bohart and Menke, 1976:30 (facial portrait), 305 (illustration of propodeal dorsum), 307 (illustration of male genitalia and sternum VIII), 308 (in checklist of world Sphecidae).

Species Identification. The unique thorax color pattern described in the otherwise very short original description allows unequivocal recognition of this species. The redescription of the type by Guiglia (1948) helps in identification.

Recognition. The female of *Paranysson abdominalis* is unique in having the pygidial plate finely rugose except basally (Fig. 8). Unlike *P. brevispinosus* and *P. melanopyrus*, but like *P. quadridentatus*, its flagellomere I is 2.2-2.4 as long dorsally as wide apically (rather than 1.4-1.7 ×). Unlike *P. quadridentatus*, the hindcoxal spine (Fig. 7) is shorter than the hindcoxal venter (at least as long as the hindcoxal venter in *P. quadridentatus*).

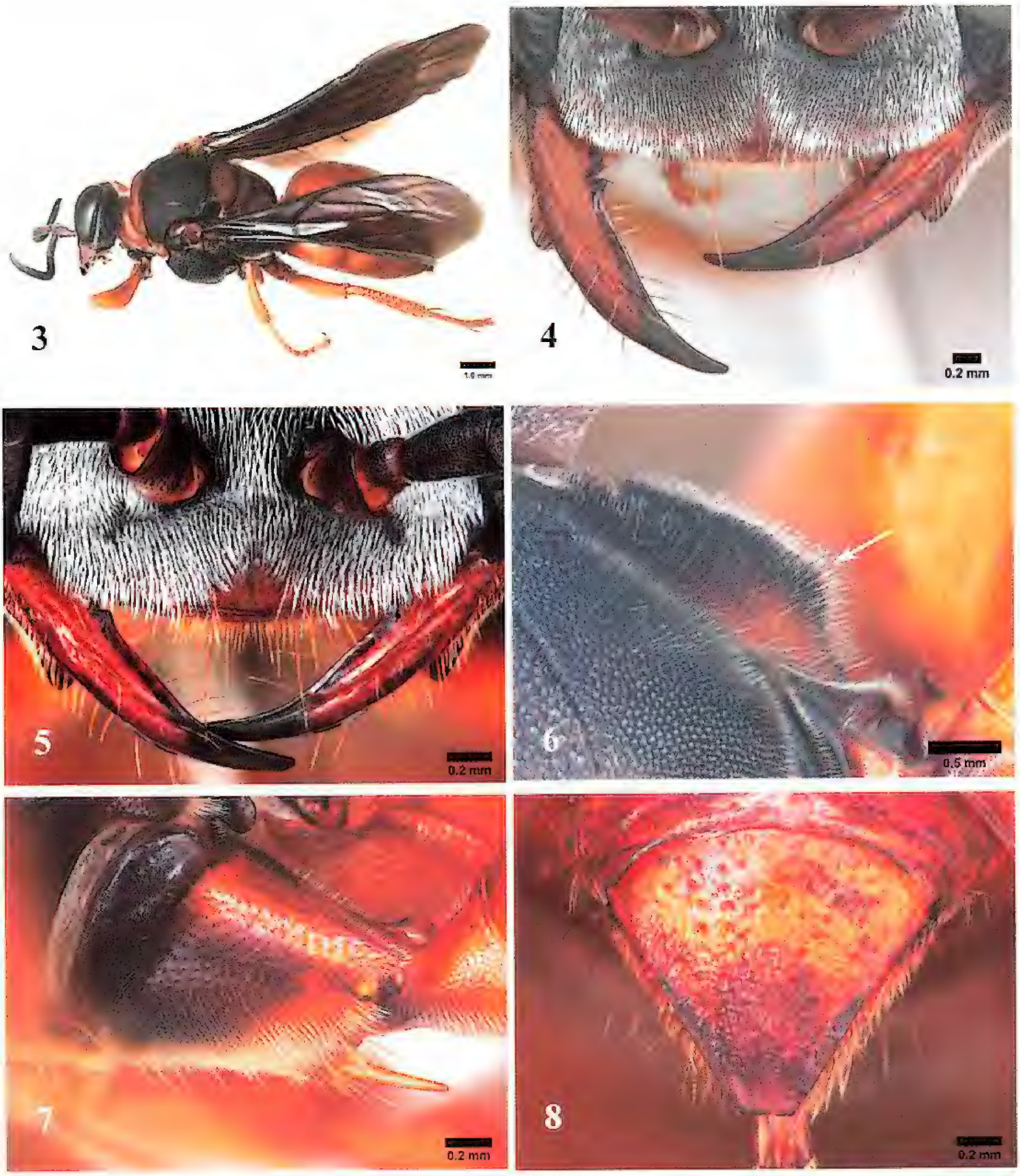
The male is unique in having flagellomere I distinctly concave ventrally (Fig. 9), whereas it is slightly flattened ventrally and at most minimally concave in the other *Paranysson*.

A subsidiary recognition feature of this species (shared with *P. quadridentatus*) is the longitudinal carina between the propodeal side and the posterior surface that is broadened at about two thirds of length (Fig. 6), but in most specimens not forming a tooth.

Unlike its congeners and unlike the specimens from Ethiopia, Kenya, and Tanzania, the populations from Senegal, Mali, and Niger have the scutellum posteriorly, the postscutellum, and often a part of the mesopleuron and propodeal enclosure ferruginous, a unique such coloration in the genus.

Justification of New Synonymy. The holotype of *Pseudohelioryctes foxii* is a male, not a female as stated in the original description. It is a typical representative of *Paranysson abdominale* with an all-black thorax, with a unique flagellomere I, and a broadened but not dentate carina between the propodeal side and posterior surface. It took this synonymy more than 120 years to be established!

Description. Clypeal lamella with one tooth on each side in most females, second ill-defined tooth present in some specimens; in male mostly without teeth, with one or two ill-defined teeth in some specimens; free margin of lobe nearly rectilinear, bevel broadened and convex mesally to



FIGURES 3-9. *Paranysson abdominalis* (Guérin-Méneville). (3) Whole body of female in oblique lateral view; (4) Female clypeus and mandible; (5) Male clypeus and mandible; (6) Posterior part of female mesopleuron and propodeal side (arrow shows the broadening of the longitudinal propodeal carina); (7) Female hindcoxa with spine; (8) Pygidial plate of female; (9) Male flagellomere I.

various degrees, extending dorsally as narrow strip. Propodeal dorsum reticulate, many cells elongate. Longitudinal carina between propodeal side and posterior surface broadened at about two thirds of length (Fig. 6), but forming tooth in some specimens.

♀ – Ocellocular distance equal to 1.0-1.1 × distance between hindocelli. Dorsal length of flagellomere I 2.2-2.4 × apical width, of apical flagellomere 1.7-1.8 × its basal width. Hindcoxal venter with spine that originates slightly before the apical hindcoxal margin; spine shorter than hindcoxal venter (Fig. 7). Pygidial plate finely rugose except basally (Fig. 8). Length 12.5-16.1 mm.

♂ – Ocellocular distance equal to 1.0-1.1 × distance between hindocelli. Flagellomere I markedly longer than flagellomere II, concave ventrally (Fig. 9), its dorsal length I 1.9 × apical width, length of apical flagellomere 1.6-1.8 × its basal width. Male terga V-VII closely punctate. Length 9.4-13.7 mm.

Geographic Distribution (Fig. 10). Known from two separate areas: one extending from Senegal to Niger, the other from Ethiopia to Tanzania.

Records. **ETHIOPIA**: six miles due north of Kulama at the north end of Lake Donaldson, an arm of Lake Stephanie, now Chew Bahir (1 ♂, ANSP, holotype of *Pseudoheliorycles foxii*).

KENYA: Eastern Province: near Ewaso Ngiro River opposite Archer's Post at 0°38.1'N 37°40.4'E (11 ♀, 5 ♂, CAS).

MALI: Mopti Region: 10 km S Mopti (16 ♀, 7 ♂, CAS; 32 ♀, 18 ♂, OÖLM).

NIGER: **Tillabéri Region**: 82 km ESE Téra at 13°51.1'N 1°31.3'E (1 ♂, CAS). **Zinder Region**: 55 km S Tanout at 14°31.2'N 8°44.3'E (6 ♂, CAS).

SENEGAL: no specific locality (Guérin-Méneville, 1844; Guiglia, 1948).

TANZANIA: Tanga Region: 2 km NE Mkomazi at 4°37.8'S 38°05.5'E (1 ♂, CAS).

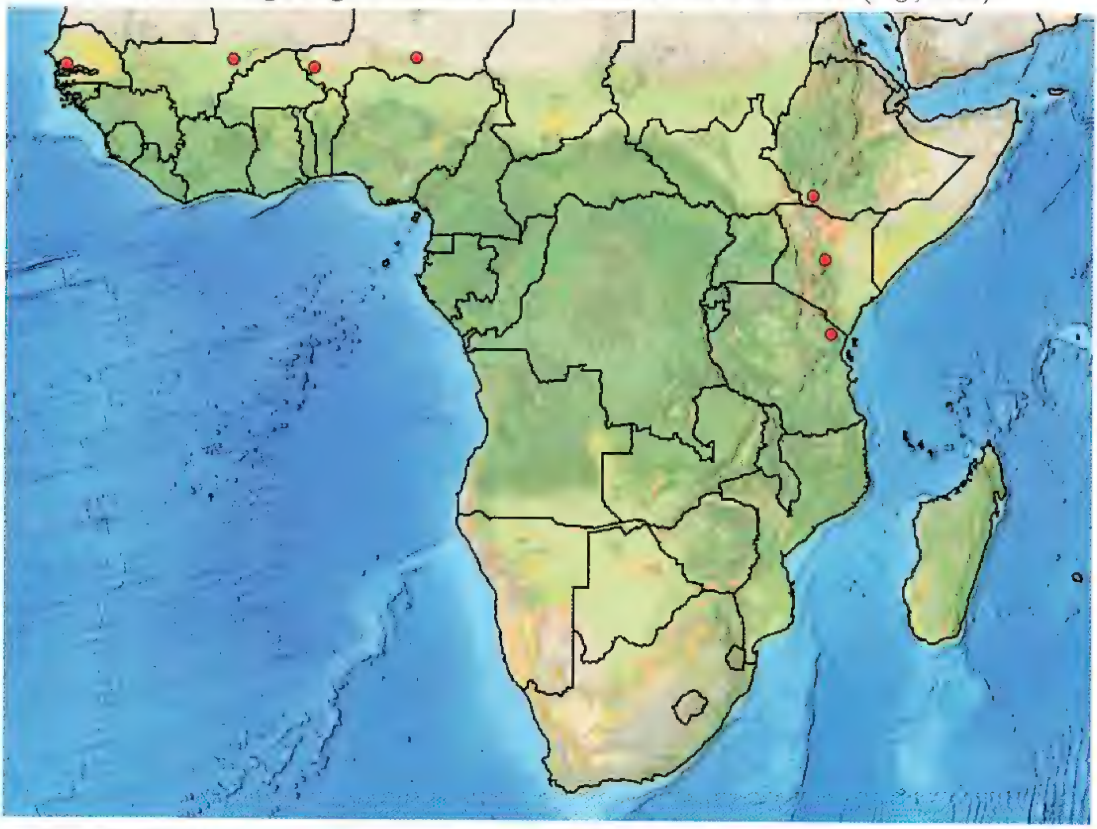


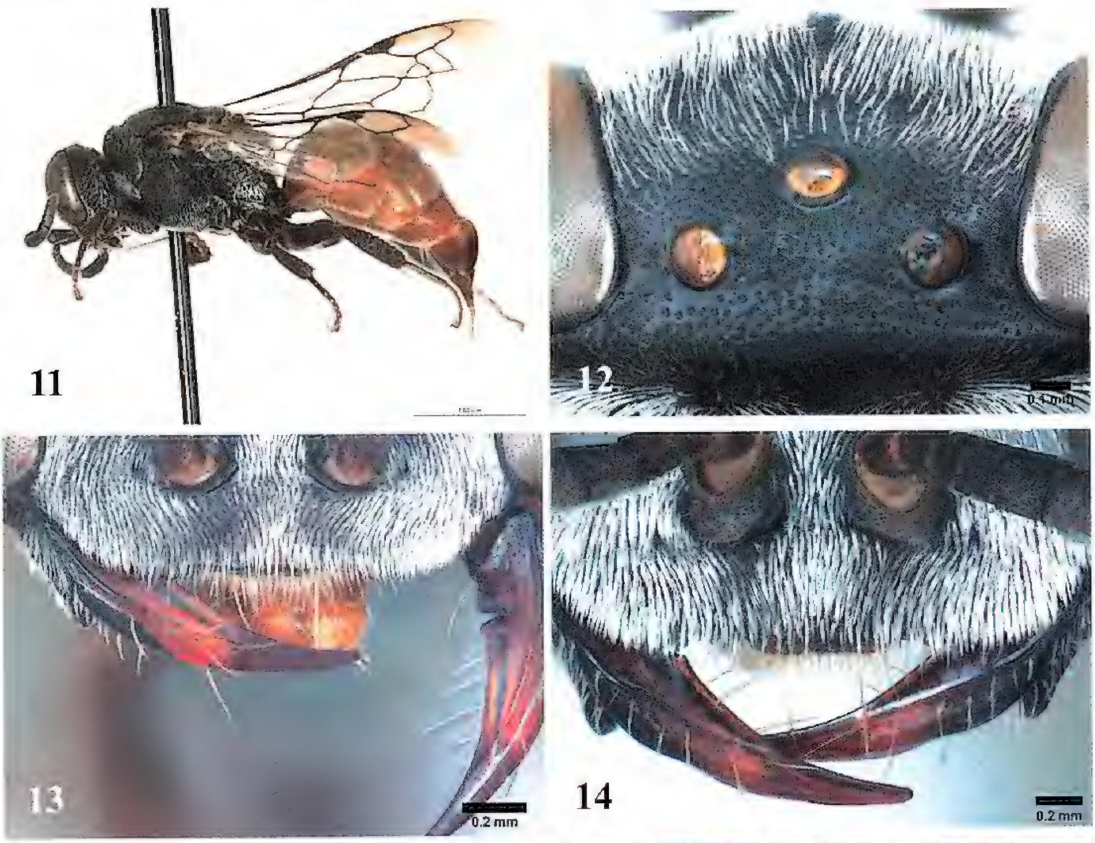
Figure 10. Collecting localities of *Paranysson abdominalis* (Guérin-Méneville).

Paranysson assimilis (Bingham)

Figures 11-16

Helioryctes assimilis Bingham, 1897:271, ♀, ♂. Lectotype: ♂, Myanmar (= Burma): Tenasserim, now Tanintharyi Region: Yunzalin River Valley (BMNH), **present designation**, examined. – Bingham, 1898:105 (Yemen: Aden). – **As *Paranysson assimilis***: R. Turner, 1914:342 (new combination, in revision of *Paranysson*); R. Bohart and Menke, 1976:308 (in checklist of world Sphecidae).

Lectotype Designation. Bingham (1897) described *Helioryctes assimilis* from the Sikkim (as Sikhim) State of India and the Tanintharyi Region of Myanmar, both males and females, but he did not designate the holotype. I have selected as the lectotype of this species a male in the BMNH



Figures 11-15. *Paranysson assimilis* (Bingham). (11) Whole body of female in lateral view; (12) Ocellar area of female showing large distance between hindocelli; (13) Female clypeus and mandible; (14) Male clypeus and mandible; (15) Female hindcoxa.

labeled "Tenasserim, Yunzalin Valley, 3. [18]91, Bingham coll.", "*Helioryctes assimilis* Bingham ♀ [*sic*], Type", apparently in Bingham handwriting, and "B.M. Type Hym. 21.1569."

RECOGNITION. *Paranysson assimilis* is the only Asian representative of the genus (all others are Afrotropical). It is characterized by its small size (the length no more than 7 mm), all black femora, ocellocular distance 0.30-0.35 × distance between hindocelli (Fig. 12), and nearly hyaline wings (Fig. 11). In the Afrotropical species, the length of most specimens is more than 7 mm, the mid- and hindfemora in the vast majority of specimens are ferruginous, ocellocular distance 0.40-1.20 × distance between hindocelli, and the wing membrane is conspicuously infumate (Fig. 3) except slightly so in some *P. helioryctoides*. Two subsidiary recognition features of *P. assimilis* are: 1. clypeus without median glabrous line extending from the bevel, Figs. 13, 14 (line present, not attaining clypeal dorsal margin in all other species except line absent in *P. melanopyrus*), and 2. the female hindcoxa with a tubercle on venter (Fig. 15), unarmed in some specimens (unarmed in *P. inermis*, with a ventral tubercle in *P. helioryctoides*, and with a conspicuous ventral spine in the other species).

DESCRIPTION. Clypeal lamella with lateral teeth varying from insignificant to well defined; bevel not extending upwards as glabrous line (Figs. 13, 14). Propodeal dorsum conspicuously reticulate, basomedian cells elongate. Longitudinal carina between propodeal side and posterior surface forming tooth at about two thirds of length. Femora all black. Terga varying from largely black to all ferruginous. Wings nearly hyaline (Fig. 11).

♀ – Ocellocular distance equal to 0.30-0.35 × distance between hindocelli. Dorsal length of flagellomere I 1.6 × apical width, of apical flagellomere 1.5-1.6 × its basal width. Hindcoxal venter with small tubercle in some specimens, but tubercle mostly rudimentary or absent (Fig. 15). Pygidial plate in most specimens rugose apically. Length 5.6-6.9 mm.

♂ – Ocellocular distance equal to 0.30 × distance between hindocelli; dorsal length of flagellomere I 1.5-1.6 × apical width, of apical flagellomere 1.3-1.4 × its basal width. Terga V and VI closely punctate, tergum VII closely to moderately sparsely punctate. Length 4.2-5.7 mm.

GEOGRAPHIC DISTRIBUTION. India and Sri Lanka to Thailand, Laos, and southern Malaysia, also recorded from Aden in south Yemen by Bingham, 1898. Unfortunately, I was not able to verify the identity of the specimen from Aden. The following subscript in Bingham, 1898:101 suggests that the specimen was deposited at the BMNH: "The present list of the Hymenoptera of Aden has been compiled from pencil notes made by me at the British Museum while I was working out Colonel Yerbury's and Capt. Nurse's collections". Actually, no such specimen can be found in the BMNH collection, as Dr. Joseph Monks, Curator of Hymenoptera, informed me on 3 November 2021.

RECORDS. **INDIA: Puducherry** (= Pondicherry): Karikal (1 ♀, CAS).

LAOS: Khammouan Province: Nakai (1 ♀, CAS).

MALAYSIA: Johor (= Johore): Mawai (1 ♀, CAS), Kampung Semangar (9 ♀, 3 ♂, CAS), Kota Tinggi (1 ♀, CAS). **Pahang**: Lata Lembik at 3°56′N 101°38′E (3 ♀, OÖLM). **Perak:** 5 km E Tanjong Rambutan (2 ♀, OÖLM).

MYANMAR: Kayin Region: Yunzalin [River] (1 ♀, USNM). **Tanintharyi Region**: Yunzalin River Valley (1 ♂, BMNH, lectotype of *Helioryctes assimilis*).

SRI LANKA: Mannar District: Kokmotte Bungalow 0.5 mi. NE Wilpattu National Park (1 ♀, CAS; 1 ♀, USNM), Kondachchi (2 ♀, CAS), Ma Villu (2 ♀, USNM), Silvatturai (7 ♀, USNM). **Monaragala District**: 13 mi. E Uda Walawe (1 ♀, CAS; 1 ♀, USNM). **Trincomalee District**: Trincomalee: China Bay Ridge Bungalow (1 ♀, USNM). **Vavuniya District**: Parayanalankulam Irrigation Canal 25 mi. NW Medawachchiya (1 ♀, CAS).

THAILAND: Chiang Mai Province: Chiang Mai (1 ♂, CAS). **Kanchanaburi Province**: dry

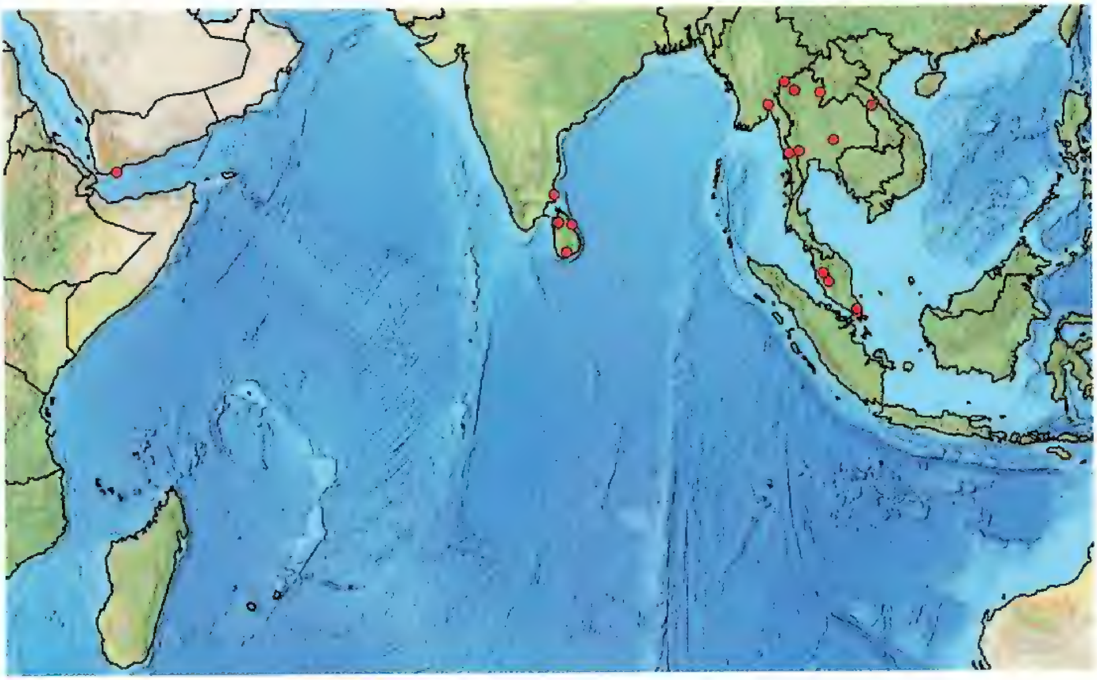


FIGURE 16. Collecting localities of *Paranysson assimilis* (Bingham).

bed of Lam Ta Pen River 5 km NW Lat Ya (2 ♂, CAS). **Mae Hong Son Province**: near Soppong (1 ♂, CAS). **Nakhon Ratchasima Province**: Nakhon Ratchasima (1 ♀, USNM). **Nan Province**: entrance to Mae Charim National Park at 18°36′0″N 100°58′34″E (2 ♀, OÖLM).

YEMEN: Aden (Bingham, 1898).

Paranysson brevispinosus Arnold

Figures 17-21.

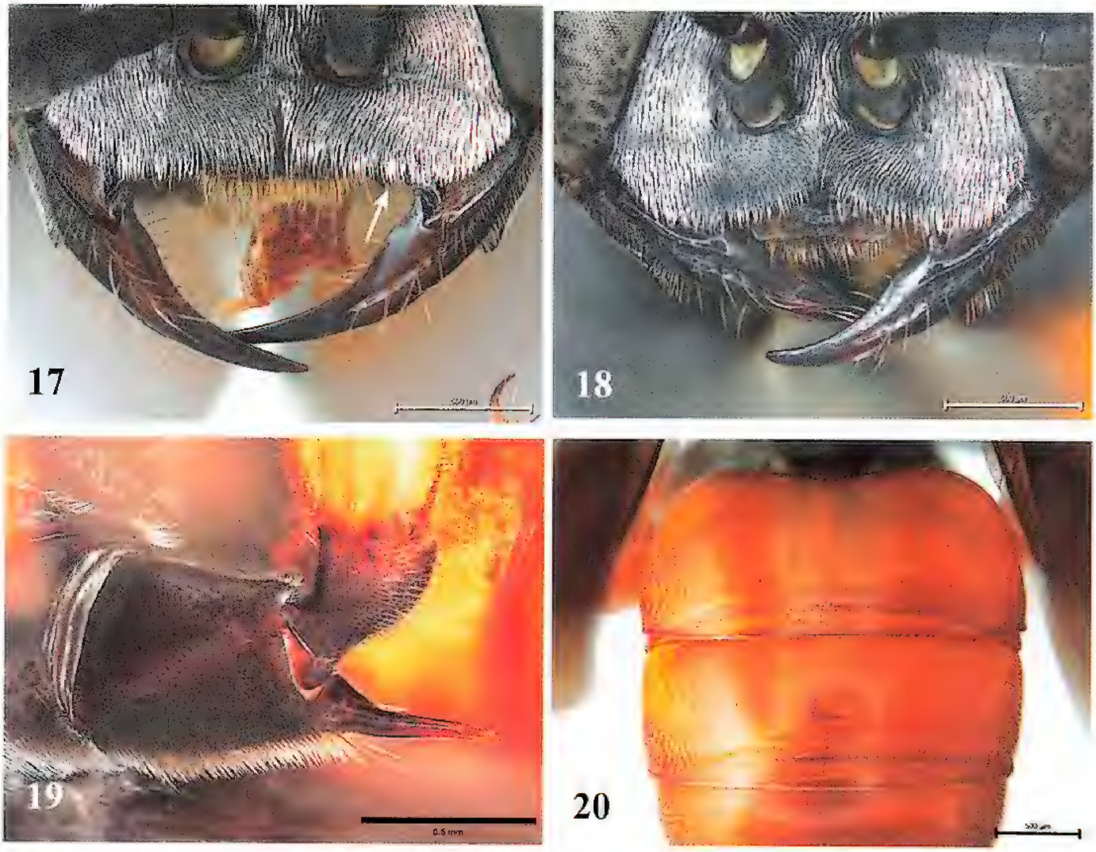
Paranysson brevispinosus Arnold, 1929:391, ♀. Holotype: ♀, Zimbabwe: Sawmills (SAM), examined. – Arnold, 1930:7 (in checklist of Afrotropical Sphecidae); Leclercq, 1968:84 (in revision of African *Paranysson*; description of ♂; Democratic Republic of the Congo); R. Bohart and Menke, 1976:308 (in checklist of world Sphecidae).

RECOGNITION. The female of *Paranysson brevispinosus* is unique in having the hindcoxal spine that originates at the apical hindcoxal margin (Fig. 19). The clypeal teeth that protrude beyond the free margin between them constitute a subsidiary recognition feature (Fig. 17). The male is characterized by its tergum II impunctate basomedially or with a few, sparse punctures (Fig. 20), also a unique character; in large specimens, the hindcoxal venter is extended as an apical tooth on the inner side.

SEX ASSOCIATION. I agree with the sex association made by Leclercq (1968) because both sexes were collected together at several localities, where no other *Paranysson* were present.

DESCRIPTION. Clypeal lamella with two teeth at each side. Propodeal dorsum reticulate, basomedian cells elongate. Longitudinal carina between propodeal side and posterior surface either forming tooth at about two thirds of length or only broadened there. Both males from Gashaka Gumti National Park, Nigeria, have the legs entirely black.

♀ – Ocellocular distance equal to 0.9-1.2 × distance between hindocelli. Lateral clypeal teeth protruding beyond free clypeal margin between them (Fig. 17). Dorsal length of flagellomere



FIGURES 17-20. *Paranysson brevispinosus* Arnold. (17) Female clypeus and mandible (arrow shows lateral clypeal tooth); (18) Male clypeus and mandible; (19) Female hindcoxa with spine; (20) Basal terga of male.

I 1.6-1.7 × apical width, of apical flagellomere 1.6-1.7 × its basal width. Hindcoxal venter with spine that originates at apical hindcoxal margin; spine markedly shorter than hindcoxal venter (Fig. 19). Pygidial plate with punctures fine, sparse, to conspicuous, dense, in most specimens with fine, longitudinal ridges next to apex. Length 12.2-13.4 mm.

♂ – Ocellocular distance equal to 0.7-0.9 × distance between hindocelli; dorsal length of flagellomere I 1.1-1.4 × apical width, of apical flagellomere 1.5-1.7 × its basal width. In large specimens, hindcoxal venter extended as apical tooth on inner side. Tergum II impunctate basomedially or with a few, sparse punctures (Fig. 20). Tergum V sparsely punctate mesally, terga VI and VII closely so. Length 8.8-11.7 mm.

GEOGRAPHIC DISTRIBUTION (Fig. 21). Burkina Faso to South Africa.

RECORDS. **BURKINA FASO: Nahouri Province**: 8 mi. N Pô (1 ♀, CAS).

CENTRAL AFRICAN REPUBLIC: 70 km NNE Bangui at 4°57′N 18°46′E (1 ♀, 2 ♂, OÖLM), 85 km NW Bangui at 4°46′N 18°04′E (1 ♂, OÖLM), 60 km SE Bouar at 5°42′N 16°00′E (1 ♀, OÖLM).

DEMOCRATIC REPUBLIC OF THE CONGO (Leclercq, 1968): **Lualaba** Province: Kapanga. **Mongala** Province: Binga. **Sankuru** Province: Madibi at 4°18′00″S 18°24′00″E. **Province unknown**: Kalani River,

MALAWI: Southern Region: Mulange at 16°01′33″S 35°30′29″E (1 ♀, UCD, as Mlange).

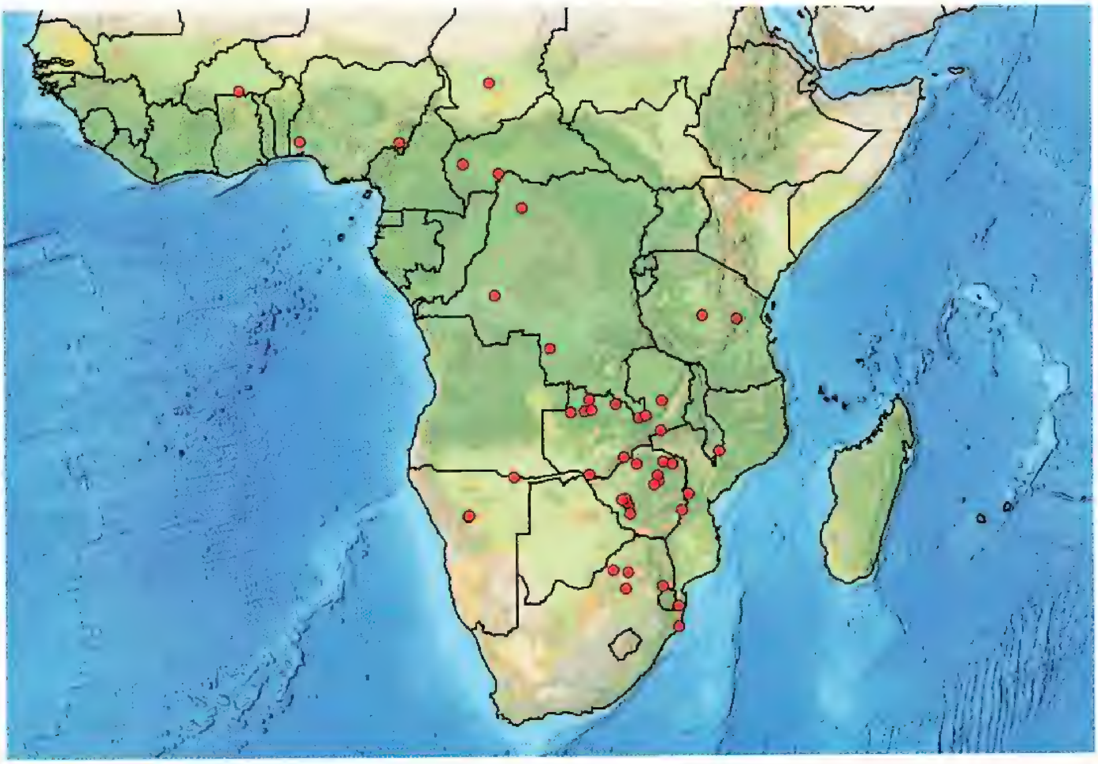


FIGURE 21. Collecting localities of *Paranysson brevispinosus* Arnold.

MOZAMBIQUE: **Manica Province**: 35 km SW Chimoio at 19°08′S 33°09′E (1 ♀, 4 ♂, OÖLM).

NAMIBIA: **Kavango-East Region**: Rundu (1 ♀, CAS; 1 ♂, OÖLM). **Otjozondjupa Region**: 18 km NE Kalkfeld at 20°45′S 16°16′E (1 ♀, CAS), 44 km SW Otjiwarongo at 20°37′S 16°22′E (1 ♂, CAS).

NIGERIA: **Oyo State**: Olokemeji [Forest Reserve] near Ibadan at 7.42°N 3.55°E (1 ♀, USNM). **Taraba State**: Gashaka Gumti National Park at 7°20′N 11°13′E (1 ♀, 2 ♂, OÖLM).

SOUTH AFRICA: **Gauteng**: Wapadrand 8 km E Pretoria at 25°48′S 28°22′E (1 ♀, CAS). **Kwazulu-Natal**: Saint Lucia Estuary (1 ♀, AMNH), Tembe Elephant Park at 27°02′S 32°23′E (1 ♀, OÖLM). **Limpopo**: Modimolle at 24°40′S 28°30′E (3 ♀, 2 ♂, OÖLM, as Nylstroom), Thabazimbi (1 ♀, OÖLM). **Mpumalanga**: 20 km NE Barbeton (1 ♂, OÖLM).

TANZANIA: **Morogoro Region**: 128 road km NW Morogoro at 6°08.2′S 36°54.3′E (1 ♀, CAS). **Singida Region**: 20 mi. SW Itigi (3 ♀, CAS).

ZAMBIA: **Central Province**: near Mkushi (1 ♀, CAS), 40 km SW Serenje (1 ♀, OÖLM). **Copperbelt Province**: 25 km W Chingola (1 ♀, OÖLM). **Eastern Province**: 42 km SW Petauke at 14°30′S 31°02′E (1 ♀, CAS). **Lusaka Province**: 120 km S Lusaka (1 ♀, OÖLM). **Muchinga Province**: 70 km S Mpika at 12°18′S 31°07′E (1 ♀, OÖLM). **Northwestern Province**: NW Kasempa at 13°06′S 25°14′E (1 ♀, OÖLM), 150 km S Mwinilunga at 13°11′S 24°14′E (1 ♂, OÖLM), 100 km W Solwezi at 12°13′S 25°39′E (1 ♂, OÖLM), 150 km SW Solwezi at 13°02′S 25°45′E (1 ♀, OÖLM). **Southern Province**: 30 km W Livingstone (1 ♀, OÖLM).

ZIMBABWE: **Bulawayo Province**: Bulawayo airport at 20°00′S 28°38′E (4 ♀, 1 ♂, CAS). **Manicaland Province**: 12 mi. S Chipinge (1 ♀, CAS). **Mashonaland Central Province**:

Mavuradonha Wilderness Area 15 km SE Muzarabani (1 ♀, 3 ♂, OÖLM), 25 km NE Shamva at Nyagui River (1 ♀, OÖLM). **Mashonaland East Province:** Beatrice near Ngezi (1 ♀, OÖLM). **Mashonaland West Province:** 30 km W Harare (3 ♂, OÖLM), Masanga 70 km W Karoi (1 ♀, OÖLM), circa 80 km NE Kwekwe (1 ♀, OÖLM). **Matabeleland North Province**: 60 km NNW Bulawayo (1 ♂, OÖLM), 90 km NW Bulawayo (1 ♂, OÖLM), Sawmills (Arnold, 1929). **Matabeleland South Province**: Matopo (1 ♀, OÖLM).

Paranysson helioryctoides (R. Turner)

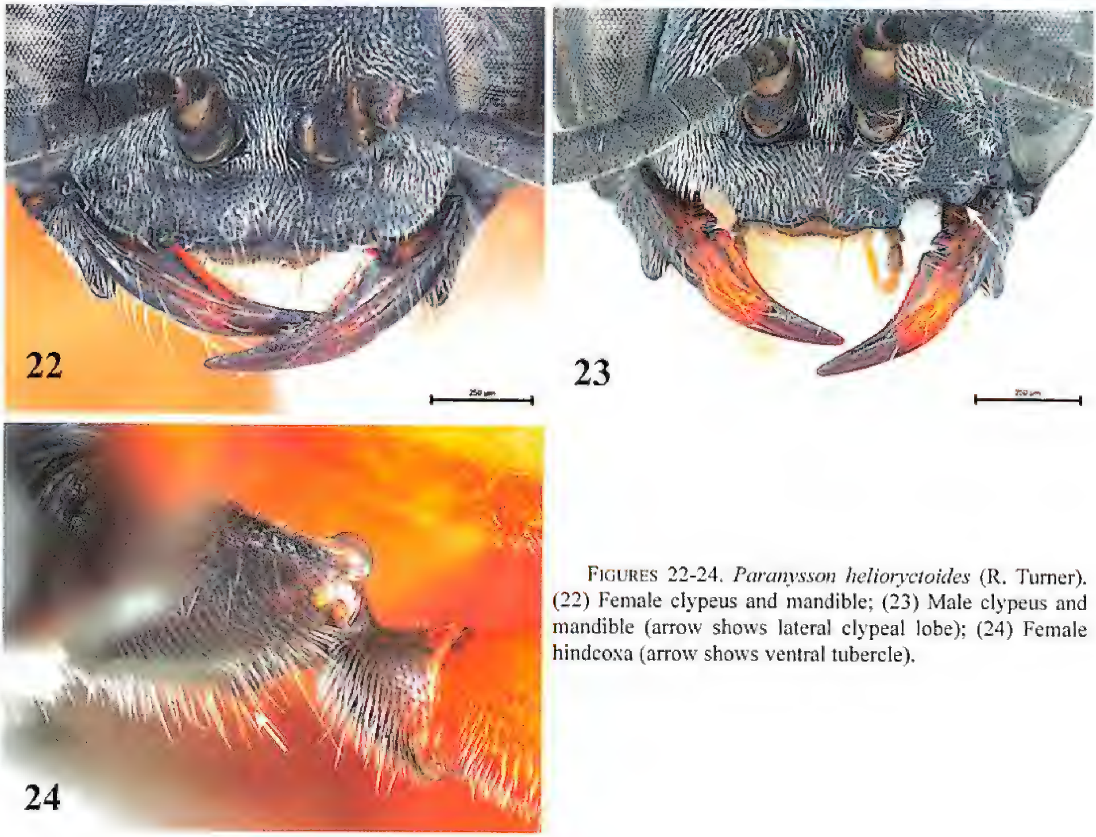
Figures 22-25.

Nysson helioryctoides R. Turner, 1912:416, ♀. Lectotype: ♀, Zambia: Pakasa, locality of unknown location (BMNH), **present designation**, examined. – **As *Paranysson helioryctoides***: R. Turner, 1914:342 (new combination, in revision of *Paranysson*); Arnold, 1923:15 (in revision of African *Paranysson*), 1930:7 (in checklist of Afrotropical Sphecidae); Leclercq, 1968:86 (in revision of African *Paranysson*); R. Bohart and Menke, 1976:296 (illustration of forewing), 308 (in checklist of world Sphecidae).

Paranysson bumbanus Leclercq, 1968:84, ♀. Holotype: ♀, Democratic Republic of the Congo: Mongala Province: Bumba (MRAC), examined. **New synonym**. – R. Bohart and Menke, 1976:308 (in checklist of world Sphecidae).

Lectotype Designation. Turner (1912) did not mention the number of specimens upon which he based his description of *Nysson helioryctoides*. I have selected as the lectotype of this species a female in the BMNH labeled "N. Rhodesia, Pakasa, 23-I-[19]11, Silverlock coll., 1912-20", "*Nysson helioryctoides*. Type" in Turner's handwriting and "B.M. Type Hym. 21.1566."

Recognition. *Paranysson helioryctoides* is the smallest among its African congeners, meas-



Figures 22-24. *Paranysson helioryctoides* (R. Turner). (22) Female clypeus and mandible; (23) Male clypeus and mandible (arrow shows lateral clypeal lobe); (24) Female hindcoxa (arrow shows ventral tubercle).

uring 6.8-8.3 mm in length in the female and 5.8-6.0 mm in the male. The female shares with some *P. assimilis* the presence of a sharp tubercle on the hindcoxal venter, but has no spine. If differs from *P. assimilis* by a number of character given under that species. Its clypeus (Figs. 22, 23), with the bevel separated by a sharp carina from the basal clypeal portion, is a subsidiary recognition feature.

The male of *P. helioryctoides* has a unique clypeus, whose free margin of the lateral lobe is obtusely angulate (Fig. 23). The free margin of the middle clypeal section is variable.

Justification of New Synonymy. When describing *P. bumbanus*, Leclercq (1968) had no specimens of *P. helioryctoides* for comparison and relied only on R. Turner's descriptions of 1912 and 1914. He quoted that author as saying that in *P. helioryctoides* "the posterior ocelli [are] nearly twice as far from each other as from the eyes", whereas in *P. bumbanus* the posterior ocelli were minimally more from each other than they were from the eyes. Indeed, in the holotype of *P. bumbanus* the ocellocular distance is equal to 0.9 of that between the hindocelli, whereas it is 0.5-0.7 in the other specimens examined. I regard this difference, however, as individual or geographic variation, as the other characters (in particular the body size, clypeus, propodeal lateral spine, and hindcoxal tubercle) are identical. Therefore, I treat these two names as synonyms.

Description. Clypeal lamella either without lateral teeth, or with one or two ill-defined teeth at each side. Propodeal dorsum reticulate, basomedian cells elongate to equilateral. Longitudinal carina between propodeal side and posterior surface forming tooth at about two thirds of length.

♀ – Ocellocular distance equal to 0.6 × distance between hindocelli. Lateral teeth of clypeal free margin rudimentary. Dorsal length of flagellomere I 1.5-1.6 × apical width, of apical flagellomere 1.5-1.6 × its basal width. Hindcoxal venter with tubercle originating at about ⅔ length of hindcoxal venter to slightly before its apical margin (Fig. 24). Pygidial plate unsculptured. Length 6.8-8.3 mm.

♂ – Ocellocular distance equal to 0.5 × distance between hindocelli; dorsal length of flagellomere I 1.4 × apical width, of apical flagellomere 1.4-1.5 × its basal width. Terga V-VII closely punctate. Length 5.8-6.0 mm.

Geographic Distribution (Fig. 25). Democratic Republic of Congo and Kenya to South Africa.

Records. **ANGOLA: Cuanza Sul Province**: Porto Amboin (1 ♀, UCD).

DEMOCRATIC REPUBLIC OF THE CONGO: Mongala Province: Bumba (1 ♀, MRAC, holotype of *Paranysson bumbanus*).

KENYA: Coast Province: Karacha forest 16 mi. N Kilifi (1 ♀, CAS), Voi (1 ♀, OÖLM), Voi: Tsavo (2 ♀, OÖLM). **Eastern Province**: W Mwingi (1 ♀, OÖLM). **Rift Valley Province**: Marich Pass Field Studies Centre at 1°32.2'N 35°27.4'E (1 ♀, 1 ♂, CAS).

MALAWI: Southern Region: Lake Chilwa (1 ♀, USNM).

SOUTH AFRICA: Kwazulu-Natal: Saint Lucia Estuary (1 ♀, AMNH). **Limpopo**: Bela-Bela (1 ♀, USNM, as Warmbad).

TANZANIA: Coast (= Pwani) **Region**: 15 km W Kibiti at 7°47'S 38°49'E (3 ♂, OÖLM), Pugu forest near Kisarawe at 6°53.6'S 39°05.9'E (2 ♂, CAS), 15 km E Utete at 8°03'S 38°53'E (1 ♂, OÖLM). **Morogoro Region**: 48 km W Morogoro at 6°56.9'S 37°20.2'E (2 ♂, CAS), 62 road km SW Morogoro at 7°02.5'S 37°15.3'E (1 ♂, CAS), Ruaha river bank 7 km S Mikumi at 7°27.4'S 37°00.5'E (1 ♀, CAS). **Tanga Region**: 10 km WNW Mabokweni at 4°59.6'S 38°59.0'E (1 ♂, OÖLM).

ZAMBIA: Central Province: 25 km SSW Kapiri Mposhi at 14°10'S 28°36'E (1 ♂, CAS). **Northwestern Province**: 150 km S Mwinilunga at 13°11'S 24°14'E (1 ♂, OÖLM). **Location unknown:** Pakasa (1 ♀, BMNH, lectotype of *Paranysson helioryctoides*).

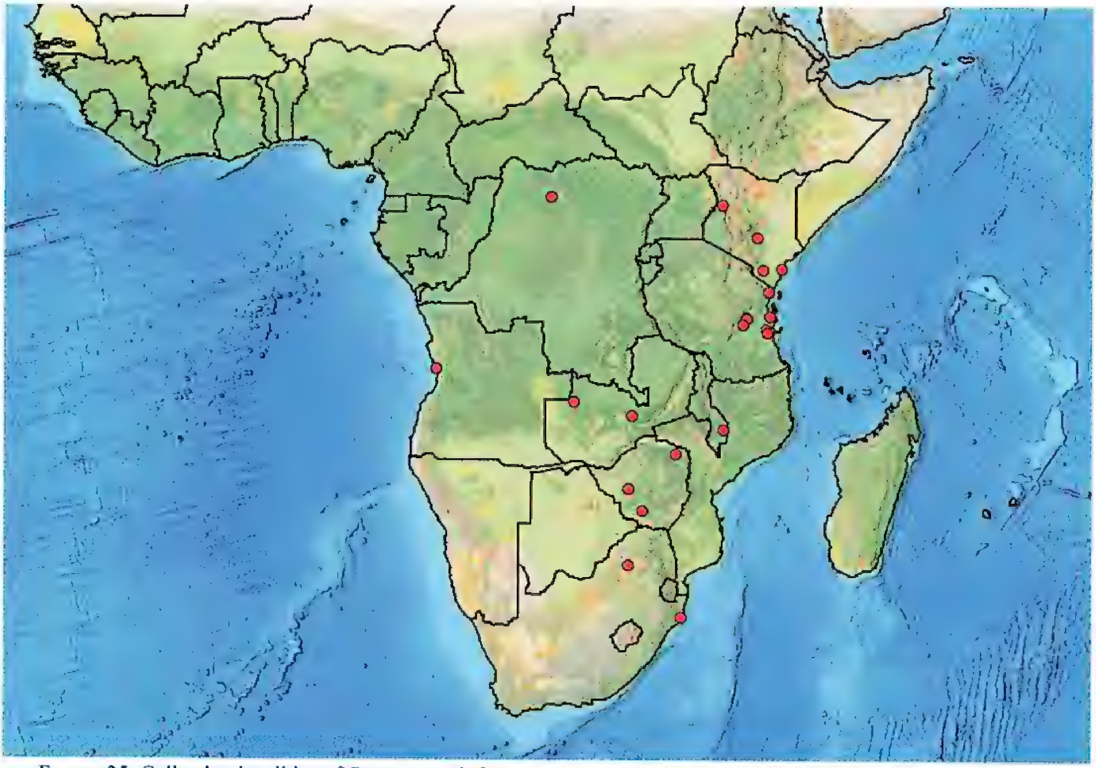


FIGURE 25. Collecting localities of *Paranysson helioryctoides* (R. Turner).

ZIMBABWE: Mashonaland Central: 25 km NE Shamva at Nyagui River (1 ♀, 2 ♂, OÖLM). **Matabeleland North**: 90 km NW Bulawayo (1 ♀, OÖLM). **Matabeleland South**: Tshabezi (1 ♂, OÖLM, as West Nicholson).

Paranysson inermis **Leclercq**
Figures 26-32.

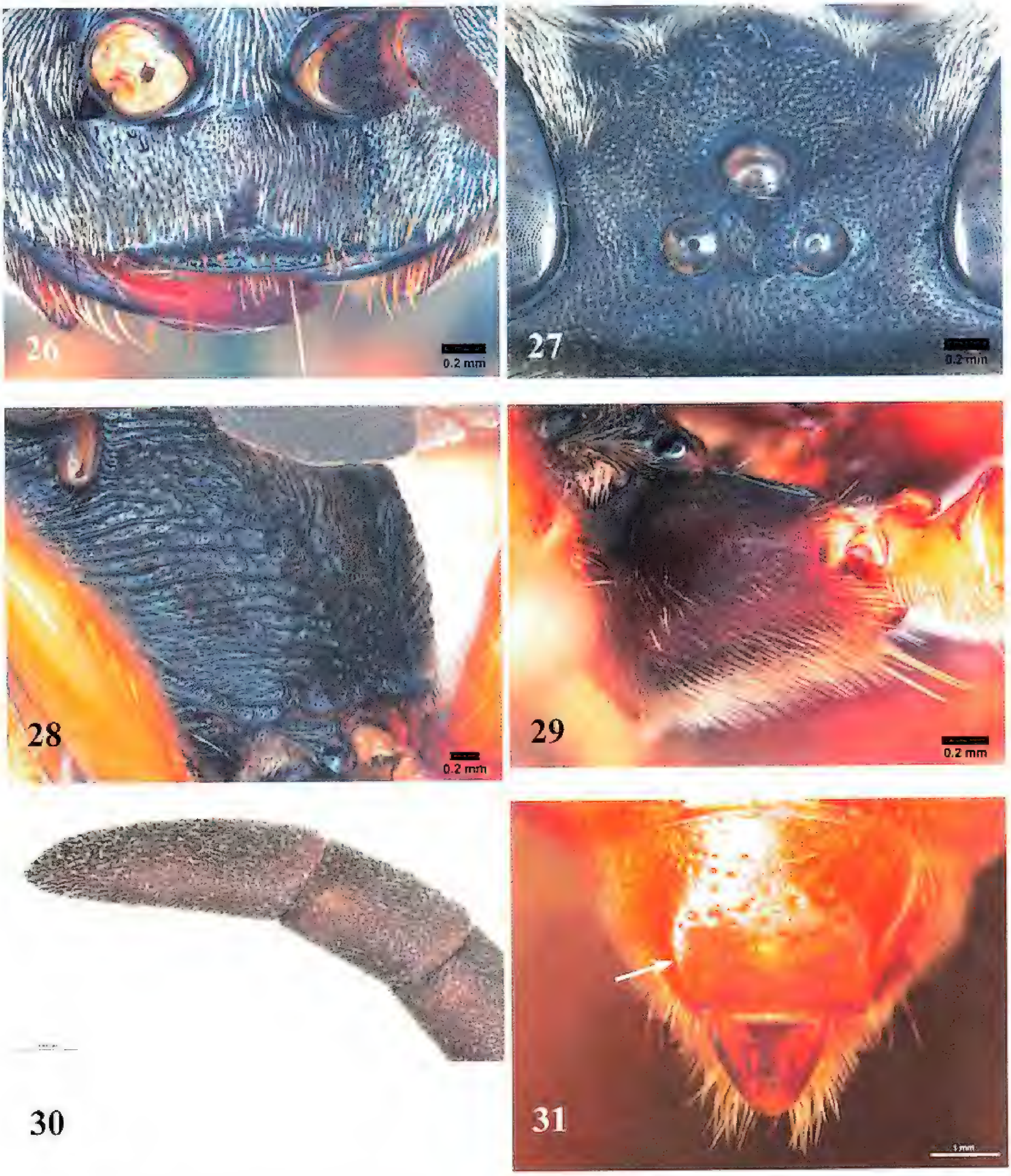
Paranysson inermis Leclercq, 1968:86, ♀, Democratic Republic of the Congo: Sud-Ubangi Province: Yambata (MRAC), examined. – Bohart and Menke, 1976:308 (in checklist of world Sphecidae).

RECOGNITION. *Paranysson inermis* differs from its congeners by its unusually long apical flagellomere (Fig. 30) whose length is 2.6 × its basal width (2.0-2.2 in *P. oscari*, and less than that in the other species). The propodeum lacking the longitudinal carina between the side and posterior surface (Fig. 28) is shared only with most specimens of *P. oscari*.

The female has two other distinctive characters: the clypeal free margin without lateral teeth (Fig. 26), and the hindcoxal venter unarmed, without tubercle or spine (Fig. 29).

The male is unique in having a narrow, triangular, unsculptured pygidial plate (Fig. 31). Two characters are subsidiary recognition features shared only with *P. oscari*: sparsely punctate terga V-VII, and an obtuse lateral carina on tergum VI (Fig. 31).

DESCRIPTION. Clypeal lamella without lateral teeth (Fig. 26), bevel separated from basal clypeal part by sharp carina (carina reduced mesally). Propodeal dorsum essentially ridged longitudinally, ridges interconnected. Longitudinal carina between propodeal side and posterior surface lacking (Fig. 28).



FIGURES 26-31. *Paranysson inermis* Leclercq. (26) Clypeus and mandible of holotype female; (27) Ocellar area of holotype female; (28) Propodeal side of holotype female in lateral oblique view showing absence of longitudinal carina; (29) Hindcoxa of holotype female showing absence of spine; (30) Apical flagellomere of male; (31) Gastral apex of male in dorsal view (arrow shows lateral carina of tergum VI).

♀ – Ocellocular distance equal to 1.2 × distance between hindocelli (Fig. 27). Dorsal length of flagellomere I 2.2 × apical width, of apical flagellomeres 2.6 × basal width (apical flagellomere longer than the penultimate). Hindcoxal venter without tubercle or spine (Fig. 29). Pygidial plate with a few, sparse punctures. Length 16.3 mm.

♂ – Ocellocular distance equal to 1.2 × distance between hindocelli; dorsal length of flagellomere I 1.7 × apical width, of apical flagellomere 2.6 × its basal width. Terga V-VII sparsely punctate, tergum VI with lateral, obtuse carina on each side (Fig. 31), pygidial plate narrow, triangular (Fig. 31). Length 11.0-11.3 mm

GEOGRAPHIC DISTRIBUTION (Fig. 32). Known from the northern part of the Democratic Republic of the Congo, and the southwestern Central African Republic.

RECORDS. **CENTRAL AFRICAN REPUBLIC**: Poko at 3°10′N 26°50′E (1 ♂, AMNH). **Lobaye**: 150 km WNW Mbaïki at 4°03′N 17°02′E (1 ♂, OÖLM).

DEMOCRATIC REPUBLIC OF THE CONGO: **Bas-Uélé Province**: Bambesa (Leclercq, 1968). **Sud-Ubangi Province**: Libenge (Leclercq, 1968), Yambata (1 ♀, MRAC, holotype of *Paranysson inermis*). **Tshopo Province**: Kisangani at 0°30′N 25°10′E (1 ♂, CAS).

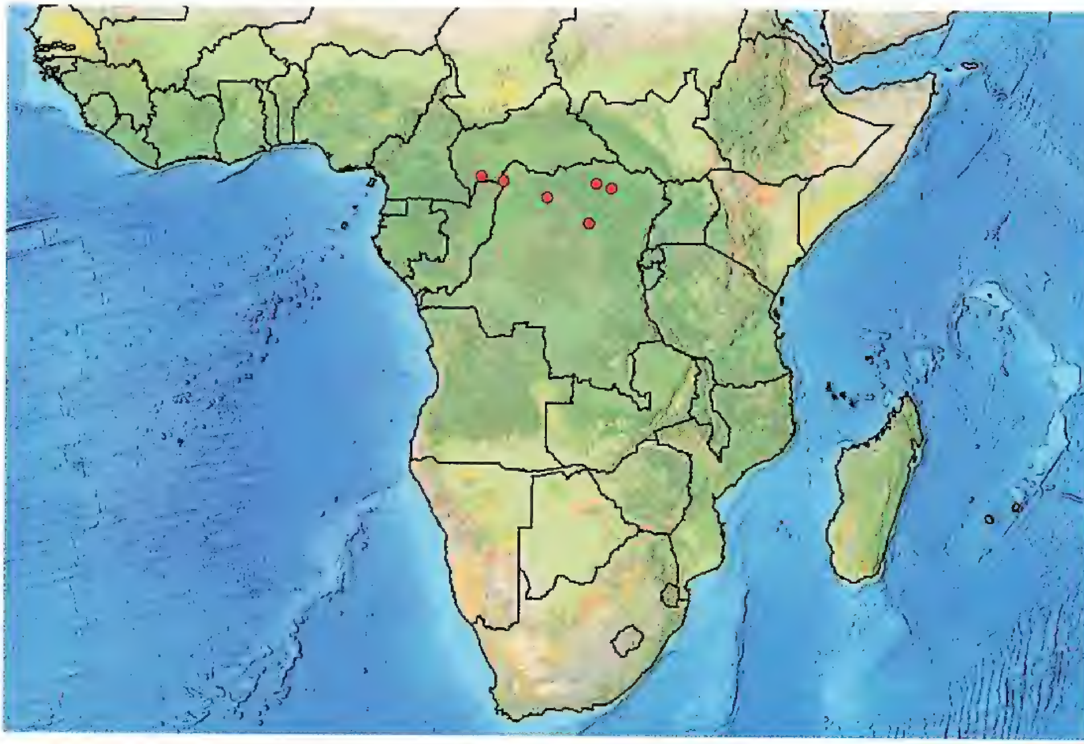


FIGURE 32. Collecting localities of *Paranysson inermis* Leclercq.

Paranysson melanopyrus **(F. Smith)**

Figures 33-36.

Helioryctes melanopyrus F. Smith, 1856:359, ♀. Lectotype: ♀, Gambia: no specific locality (BMNH), **present designation**, examined. – Walker, 1871:26 (Red Sea coast of Africa: Harkeko); nec W. Fox, 1896:554 and Magretti, 1898:49 (= *Paranysson foxii*, now *Paranysson abdominale*); Bingham, 1897:270 (redescription, incorrectly recorded from India and Myanmar); Dalla Torre, 1897:577 (in catalog of world Sphecidae); Magretti, 1898:49 (Somalia: Ganana), 1906:20 (Eritrea); Innes Bey, 1912:112 (specimens recorded by Walker, 1871, now destroyed by dermestids, were collected at Harkeko, as *melanopyga*). – As ***Paranysson melanopyrus***: R. Turner, 1912:416 (new combination, Zambia: Pakasa; individual variation), 1914:341 (in revision of *Paranysson*); Arnold, 1923:14 (in revision of African *Paranysson*), 1930:7 (in checklist of Afrotropical Sphecidae); Schouteden, 1930:92 (Democratic Republic of the Congo); Bequaert, 1933:36 (nesting in ground, prey: pentatomid *Natalicola pallidus* Westwood); Leclercq, 1968:88 (in revision of African *Paranysson*; Liberia, Democratic Republic of the Congo); R. Bohart and Menke, 1976:299 (illustration of hindcoxa and hindtibia), 305 (illustration of female pygidial plate), 308 (in checklist of world Sphecidae); Pick and Spanjer, 1986:186 (in list of Sphecidae with known prey); Dollfuss, 1990:122 (Central African Republic).

Paranysson congoensis Arnold, 1929:392, ♀, ♂. Syntypes: Democratic Republic of the Congo: Stanleyville, now Kisangani (MRAC). Synonymized with *Paranysson melanopyrus* by Leclercq, 1968:88. – Arnold, 1930:7 (in checklist of Afrotropical Sphecidae); Schouteden, 1930:92 (Democratic Republic of the Congo).

Lectotype Designation. F. Smith (1856) did not record the number of specimens upon which he based his description of *Helioryctes melanopyrus*. I have designated as the lectotype of this species a female in BMNH labeled "*Helioryctes melanopyrus* Smith, Gambia" (label handwritten, perhaps by F. Smith himself) and "BMNH Type Hym. 21.1,567)".

Recognition. The female of *Paranysson melanopyrus* differs from its congeners in having the hindcoxal spine that emerges at or before the hindcoxal midlength (Fig. 35), at or near its midline. Subsidiary recognition features are: the dorsal length of flagellomere I is 1.4-1.6 × apical width; the lateral clypeal teeth do not protrude beyond the free clypeal margin between them (Fig. 33); and in most specimens the longitudinal carina between the propodeal side and posterior surface forming a sharp tooth at about two thirds of length.

The male of *P. melanopyrus* has a distinctive clypeus whose lamella is slightly projecting and delimited on each side by a tooth (Fig. 34), but only angulate laterally in some specimens; the distance between the teeth is equal to 1.2-1.8 × midocellar diameter. Unlike *P. quadridentatus*, the dorsal length of flagellomere I equals 1.0-1.1 × that of flagellomere II (rather than 1.2-1.6 ×); and the hindcoxal venter has no preapical carina, is all punctate, not concave apically (rather than with a preapical, semicircular carina and with concave, unsculptured area between the carina and the apex).

Description. Clypeal lamella with two teeth on each side, teeth greatly reduced in many males. Propodeal dorsum reticulate, basomedian cells elongate. Longitudinal carina between propodeal side and posterior surface in most specimens forming tooth at about two thirds of length, but only broadened there in certain individuals.

♀ – Ocellocular distance equal to 0.5-0.6 × distance between hindocelli. Lateral teeth of clypeal free margin ill defined. Dorsal length of flagellomere I 1.4-1.6 × apical width, of apical flagellomere 1.7-1.8 × its basal width. Hindcoxal venter with spine originating at or before hindcoxal midlength, Fig. 35 (the difference in the spine position can be observed on the right and left hindcoxa of the same specimen); spine about as long as hindcoxal venter. Pygidial plate sparsely punctate, in many specimens microareolate. Length 8.5-13.3 mm.

♂ – Ocellocular distance equal to 0.4 × distance between hindocelli. Clypeal lamella slightly

FIGURES 33-35. *Paranysson melanopyrus* (F. Smith). (33) Female clypeus and mandible; (34) Male clypeus and mandible; (35) Female hindcoxa with spine.

projecting, delimited on each side by tooth (Fig. 34), only angulate laterally in some specimens; free margin between teeth slightly concave; distance between teeth equal to 1.2-1.8 × midocellar diameter. Flagellomere I as long as 1.0-1.2 × flagellomere II, its dorsal length 1.3-1.5 × apical width, of apical flagellomere 1.5-1.6 × its basal width. Terga V-VII closely punctate. Length 6.7-10.8 mm.

GEOGRAPHIC DISTRIBUTION (Fig. 36). Senegal and Niger to South Africa.

RECORDS. **CENTRAL AFRICAN REPUBLIC**: ca 40 km E Bambio at 3°59′N 17°11′E (2 ♂, OÖLM), ca 50 km NE Bambio at 3°59′N 17°11′E [*sic*] (3 ♀, 2 ♂, OÖLM), 70 km NNE Bangui at 4°57′N 18°46′E (3 ♀, 2 ♂, OÖLM), 85 km NW Bangui at 04°46′N 18°04′E (2 ♀, OÖLM), 50 km from Boda [*no direction*] at 4°03′N 17°20′E (2 ♀, OÖLM), 60 km SE Bouar at 5°42′N 16°00′E (1 ♀, OÖLM), 60 km W Bouar at 5°45′N 15°13′E (2 ♀, OÖLM), 90 km N Carnot at 5°36′N 15°54′E (5 ♀, 2 ♂, OÖLM), near Mbomo at 0°24′20″N 14°39′26″E (1 ♀, OÖLM), 35 km NE Nola at 3°46′N 16°13′E (2 ♂, OÖLM), 40 km S Nola at 3°23′N 16°10′E (2 ♂, OÖLM), 45 km E Nola at 3°40′N 16°26′E (2 ♀, OÖLM), 90 km NE Nola at 4°04′N 16°37′E (3 ♀, 5 ♂, OÖLM).

DEMOCRATIC REPUBLIC OF THE CONGO (localities followed by L are from Leclercq, 1968): **Bas-Uele**: Bambesa (L). **Équateur**: Eala (L). **Haut-Katanga**: Kasenga (Bequaert, 1933), Lubumbashi (L, as Elisabethville). **Haut-Ouèle**: Faradje at 3°40′N 29°40′E (1 ♀, AMNH). **Kinshasa**: Kinshasa at 4°20′S 15°20′E (2 ♀, AMNH). **Kongo-Central**: Mpese (L). **Lualaba**: Lulua (L). **Mai-Ndombe**: Bena Bendi (L), Bolobo (L), Bumbuli (L), Kunzulu (L), Wombali (L). **Maniema**: Elila (L), Kasongo (L). **Mongala**: Binga (L). **North Kivu**: 39 km S Walikale (1 ♀,

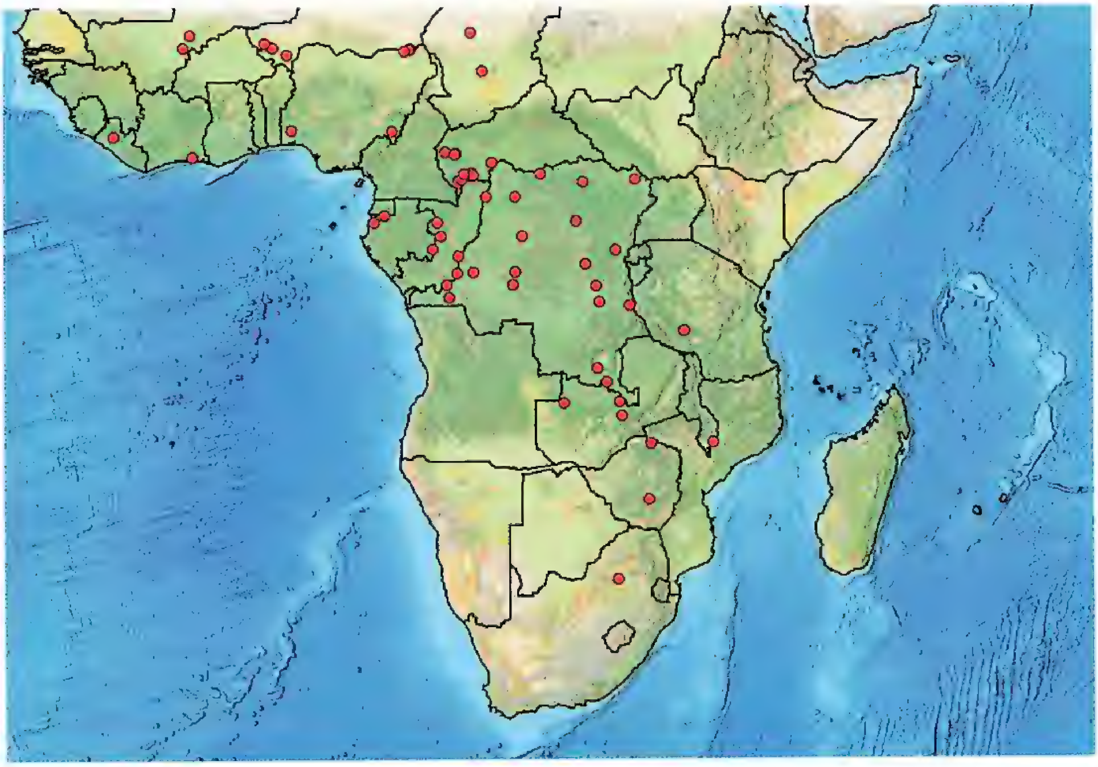


FIGURE 36. Collecting localities of *Paranysson melanopyrus* (F. Smith).

4 ♂, CAS). **Nord-Ubangi**: Yakoma (L). **Tanganika**: Lukuga River basin (L), Kalemie (institution?). **Tshopo**: Kisangani (28 ♀, 15 ♂, AMNH; 2 ♀, 1 ♂, UCD; as Stanleyville). **Tshuapa**: Bokuma at 0°40′0″S 21°1′0″E (L).

GAMBIA: no specific locality (1 ♀, BMNH, lectotype of *Heliorycies melanopyrus*).

GABON: **Haut-Ogooué Province**: Léconi (1 ♀, FSAG). **Ogooué-Ivindo Province**: Ntoum (1 ♀, FSAG). **Woleu-Ntem Province**: near Nzogbour at 0°55′36″N 10°36′17″E (1 ♀, FSAG).

IVORY COAST: **Abijan District**: Abijan: forêt de Banco (1 ♀, 1 ♂, CAS).

LIBERIA: Moala (Leclercq, 1968):

MALI: 10 km S Mopti (1 ♀, OÖLM), 30 km NE San (1 ♀, OÖLM).

MALAWI: Mulanje (1 ♀, USNM).

NIGER: **Diffa Region**: 5 km N Diffa at 13°22.2′N 12°36.4′E (1 ♀, 1 ♂, CAS), 14 km W Diffa at 13°15.8′N 12°29.0′E (1 ♀, CAS), 14 km E Maïné Soroa at 13°11.6′N 12°08.6′E (1 ♀, CAS). **Dosso Region**: 13 km S Dosso at 12°56.6′N 3°11.0′E (1 ♀, CAS). **Niamey Region**: 8 km NW Niamey at 13°35.8′N 1°59.9′E (1 ♂, CAS). **Tillabéri Region**: Malalé 10 km E Niamey at 13°27.1′N 2°10.4′E (1 ♂, CAS), 82 km ESE Téra at 13°51.1′N 1°31.3′E (1 ♂, CAS).

NIGERIA: **Oyo State**: Olokemeji [Forest Reserve] near Ibadan at 7.42°N 3.55°E (1 ♂, UCD; 1 ♀, 4 ♂, USNM). **Taraba State**: Gashaka Gumti National Park at 7°20′N 11°13′E (1 ♀, OÖLM).

REPUBLIC OF THE CONGO (= Congo Brazzaville): Oka (1 ♂, USNM).

SENEGAL: **Thiès Region**: Toubab Dialao (1 ♂, USNM).

SOUTH AFRICA: **Gauteng**: Pretoria (2 ♂, USNM).

TANZANIA: **Mbeya Region**: Mantadi village at 7°50′33″S 33°21′19″E (1 ♂, OÖLM).:

ZAMBIA: **Central Province**: 15 km S Kapiri Mposhi (1 ♀, OÖLM). **Copperbelt**: 45 km SE Kitwe (1 ♀, OÖLM). **Northwestern Province**: 150 km S Mwinilunga at 13°11'S 24°14'E (1 ♀, OÖLM).

ZIMBABWE: **Mashonaland Central Province**: Mavuradonha Wilderness Area 15 km SE Muzarabani (1 ♀, OÖLM). **Masvingo Province**: Mushandike National Park (1 ♀, OÖLM).

***Paranysson oscari* R. Turner**
Figures 37-44.

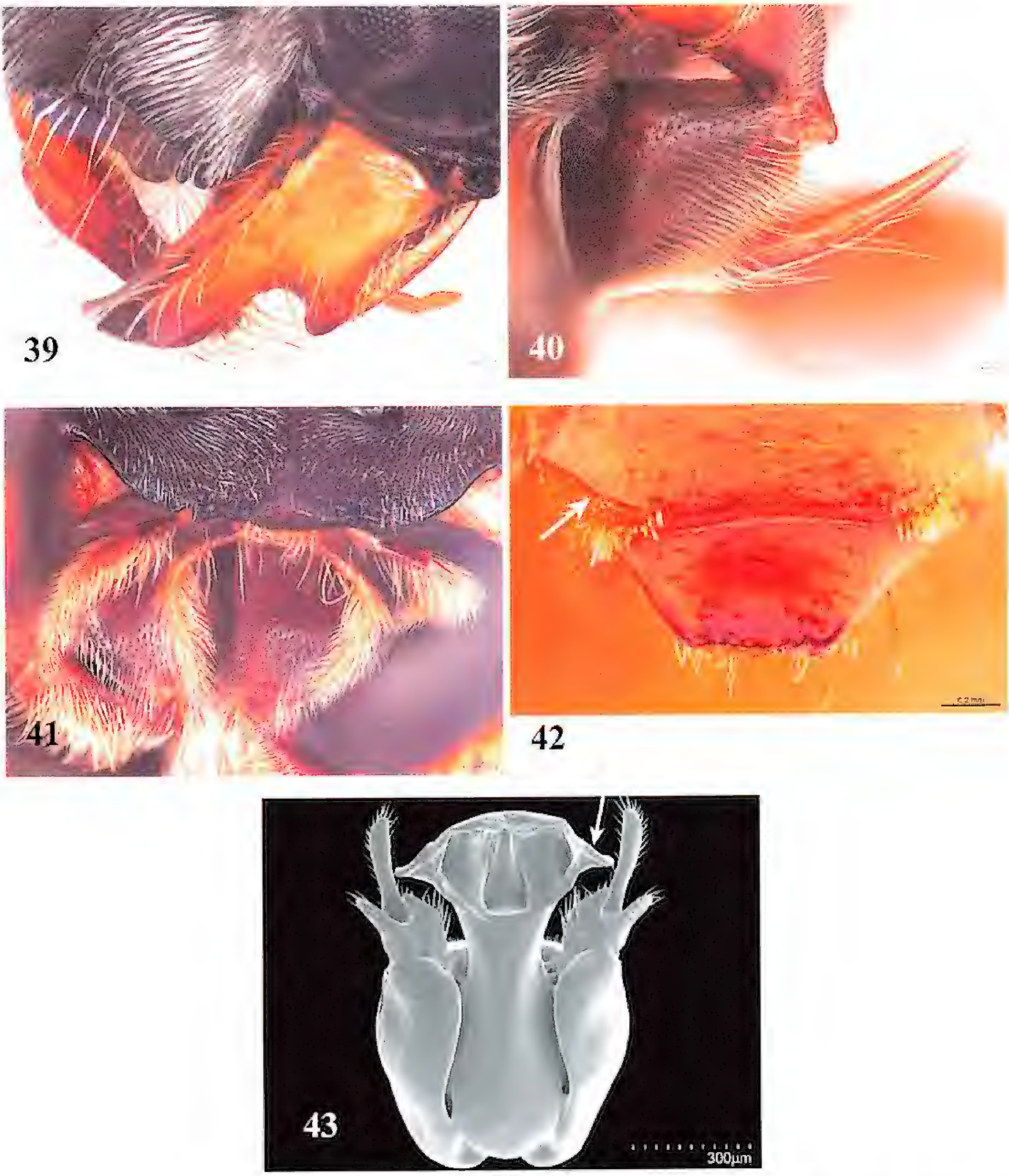
Paranysson oscari R. Turner, 1914:341, ♀. Lectotype: ♀, Zambia: Pakasa, locality of unknown location (BMNH), **present designation**, examined. – Arnold, 1923:15 (in revision of African *Paranysson*), 1930:7 (in checklist of Afrotropical Sphecidae); Schouteden, 1930:92 (Zaire); Arnold, 1951:163 (Ghana: Aburi); Leclercq, 1968:89 (in revision of African *Paranysson*; Zaire), 1969:1053 (Congo Brazzaville); R. Bohart and Menke, 1976:308 (in checklist of world Sphecidae); Dollfuss, 1990:122 (Central African Republic).

Paranysson oscari race *servus* Arnold, 1929:392, ♂. Holotype: ♂, Liberia: Paiata (MRAC, see Leclercq, 1968:89). Paratypes: Democratic Republic of the Congo: Stanleyville, now Kisangani. Synonymized with *Paranysson oscari* by Leclercq, 1968:89. – Arnold, 1930:7 (in checklist of Afrotropical Sphecidae).

LECTOTYPE DESIGNATION. R. Turner, 1914 described *Paranysson oscari* from an unspecified number of females, without designating the holotype. I have designated as the lectotype of this species a female in the BMNH labeled "N. Rhodesia, Pakasa, 25.I.[19]11, Silverlock coll., 1912-20", "*Paranysson oscari* Turn. Type" in Turner's handwriting, and "B.M. Type Hym. 21.1568."

RECOGNITION. *Paranysson oscari* differs from its congeners by several outstanding characters. First, the basal portion of the mandible (Fig. 39) is impunctate or has a few, sparse punctures (rather than being closely punctate). Also, the clypeal bevel is markedly inclined between basal part and lamella (perpendicular in some females, nearly reduced in some specimens). In the female, the ventral surface of the hindcoxal spine (Fig. 40) is sparsely setose (glabrous in the other species); in the male, the palpi are conspicuously setose (Fig. 41), terga V-VII sparsely punctate (in most specimens densely punctate apically on tergum VII), tergum VI with obtuse, lateral carina on each side (Fig. 42), as in *Paranysson inermis*, tergum VII with posterior margin truncate apically in most specimens (Fig. 42) rather than rounded or triangular. As in *P. inermis*, the propodeum in most specimens has no carina between side and posterior surface, although in some specimens an ill-defined carina is present. A subsidiary recognition feature is a long apical flagellomere, longer than in the other species except *P. inermis* (its dorsal length is 2.1-2.2 × its basal width in the female and 2.0-2.1 in the male, while 1.7-1.8 × and 1.6-1.8, respectively, in *P. abdominalis* and less than that in the other species).


37 38



FIGURES 37-43. *Paranysson oscari* R. Turner. (37) Female clypeus and mandible; (38) Male clypeus and mandible; (39) Female clypeus and mandibular base in lateral oblique view; (40) Female hindcoxa with spine; (41) Male palpi; (42) Gastral apex of male in dorsal view (arrow shows lateral carina of tergum VI); (43) Male genitalia in dorsal view (arrow shows lateral process of penis valve).

DESCRIPTION. Clypeal bevel markedly inclined between basal part and lamella (perpendicular in some females), nearly reduced in some specimens, delimited from basal part by sharp carina (Figs. 37, 38), mesally extending toward clypeal base as glabrous line that is well defined in male (Fig. 39); clypeal lamella with two teeth on each side, with only one teeth on the right side in male from Zimbabwe. Propodeal dorsum conspicuously ridged longitudinally in most specimens, reticulate in some, in most specimens without carina between side and posterior surface, with ill-defined carina in some.

♀ – Ocellocular distance equal to 1.0-1.1 × distance between hindocelli. Lateral teeth of clypeal free margin well defined, slightly protruding beyond clypeal margin between them. Dorsal length of flagellomere I 1.6-1.9 × apical width, of apical flagellomere 2.1-2.2 × its basal width. Hindcoxal spine originating closer to anterior hindcoxal margin than to posterior (Fig. 40), setose ventrally, as long as or slightly longer than hindcoxal venter. Pygidial plate impunctate to sparsely punctate, mainly laterally. Length 7.8-12.2 mm.

♂ – Ocellocular distance equal to 1.1-1.2 × distance between hindocelli; dorsal length of flagellomere I 1.7-2.0 × apical width, of apical flagellomere 2.0-2.1 × its basal width. Palpi conspicuously setose (Fig. 41). Mesothoracic venter covered with dense, appressed pilosity that completely conceals integument in oblique lateral views. Terga V-VII sparsely punctate (tergum VII in most specimens densely punctate apically), tergum VI with obtuse, lateral carina on each side (Fig. 42), as in *Paranysson inermis*, tergum VII with posterior margin truncate apically in most specimens (Fig. 42), insignificantly concave in some. Length 6.2-10.7 mm. Unlike other *Paranysson*, penis valve has a subapical lateral process (Fig. 43).

GEOGRAPHIC DISTRIBUTION (Fig. 44). Liberia and northern Cameroon in the north to northern South Africa in the south.

RECORDS. **ANGOLA: Cuanza Sul Province**: 4 mi. SW Quilenda (1 ♂, CAS).

BURUNDI: Rumonge Province: 6 mi. N Rumonge (1 ♀, 1 ♂, CAS).

CAMEROON: Nord Region: 15 km W Campement des Eléphants (= 67 km S Garoua) at 8°46.6′N 13°36.5′E (2 ♀, 1 ♂, CAS). **Sud Region**: Dja [Faunal Reserve] (1 ♀, USNM), 7 mi. S Ebolowa (1 ♂, CAS).

CENTRAL AFRICAN REPUBLIC: ca 40 km E Bambio at 3°59′N 17°11′E (1 ♀, 3 ♂, OÖLM), ca 50 km NE Bambio at 4°10′N 17°14′E (1 ♀, 2 ♂, OÖLM), 70 km NNE Bangui at 4°57′N 18°46′E (3 ♀, 4 ♂, OÖLM), 50 km SW Bangui at 4°04′N 18°14′E (2 ♂, OÖLM), Bangui-Binbo at 4°20′N 18°20′E (1 ♀, OÖLM) and 4°20′N 18°32′E (2 ♂, OÖLM), 50 km from Boda [*no direction*] at 4°03′N 17°20′E (1 ♀, 1 ♂, OÖLM), 140 km ESE Bossangoa at 6°11′N 18°22′E (1 ♀, OÖLM), 60 km SE Bouar at 5°42′N 16°00′E (2 ♀, OÖLM), 90 km S Bozoum at 5°39′N 16°37′E (1 ♀, OÖLM), 90 km N Carnot at 5°36′N 15°54′E (1 ♀, 2 ♂, OÖLM), Gashaka Gumti National Park at 7°21′N 11°32′E (1 ♀, OÖLM), 40 km S Kaga Bandoro at 6°41′N 19°07′E (1 ♀, OÖLM), 10 km NNE Mbaïki at 3°56′N 18°00′E (1 ♂, OÖLM), 20 km NNE Mbaïki at 3°04′N 18°03′E (1 ♂, OÖLM), 150 km WNW Mbaïki at 4°03′N 17°02′E (2 ♀, 5 ♂, OÖLM), 35 km NE Nola at 3°46′N 16°13′E (2 ♂, OÖLM), 40 km S Nola at 3°23′N 16°10′E (1 ♀, 2 ♂, OÖLM), 45 km E Nola at 3°40′N 16°26′E (2 ♀, 2 ♂, OÖLM) and 3°32′N 16°26′E (1 ♂, OÖLM), 90 km NE Nola at 4°04′N 16°37′E (1 ♀, 10 ♂, OÖLM) and 4°07′N 16°37′E (3 ♀, 6 ♂, OÖLM), 95 km SW Sibut at 5°12′N 18°25′E (3 ♀, 1 ♂, OÖLM).

DEMOCRATIC REPUBLIC OF THE CONGO (localities followed by L are from Leclercq, 1968): **Bas-Uélé Province**: Abumombazi (L), Amadi (L), Api (L), Bambesa (L), Dingila (L), Poko at 3°10′N 26°50′E (1 ♀, 2 ♂, AMNH). **Cuvette-Ouest Province**: 10 km SW Kéllé at 0°05′09″N 14°26′07″E (1 ♀, OÖLM). **Equateur Province**: Eala (L), Sokro (L). **Haut-Katanga Province**: 27 mi. SE Kienge (1 ♀, CAS), Lubumbashi (L, as Elisabethville), 4 mi. S Sampwe

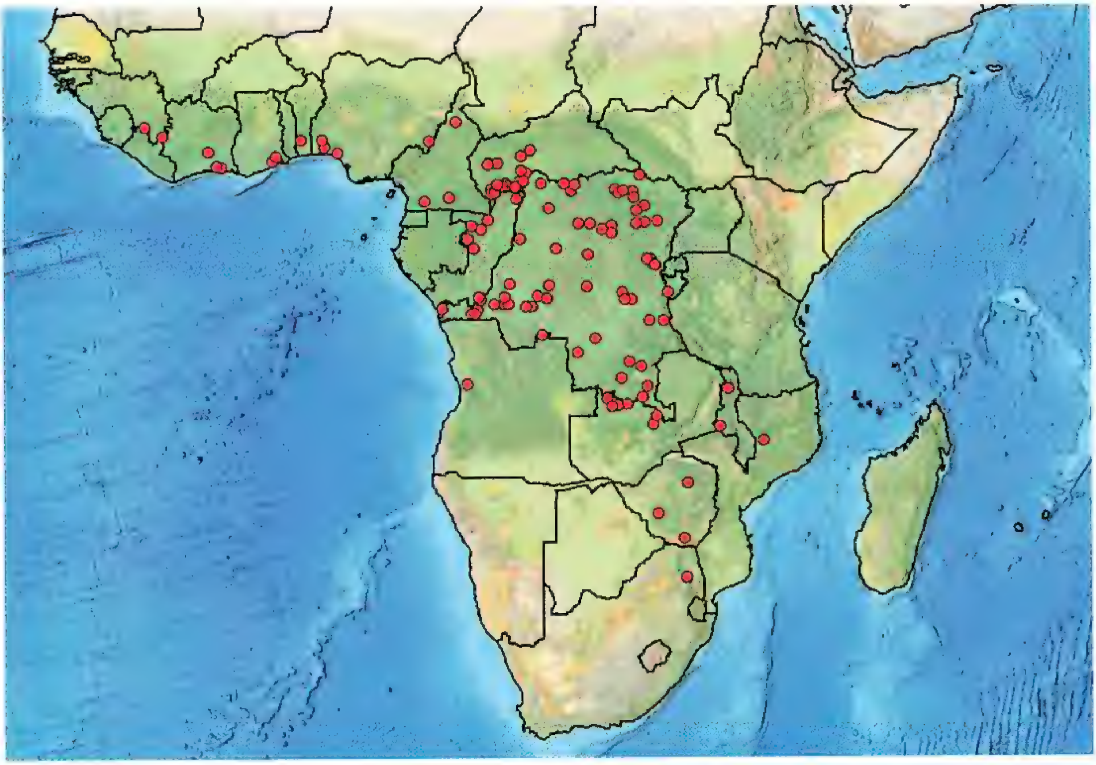


FIGURE 44. Collecting localities of *Paranysson oscari* R. Turner.

(1 ♀, CAS). **Haut-Uélé Province**: Mauda (L). **Kongo Central** (formerly Bas-Congo): Kisantu (L), Kwilu (L), Luali (L), Madimba (L), Mayidi (L), Mbanza-Ngungu at 5°30′S 15°0′E (1 ♂, AMNH, as Thysville). **Kwango Province**: Dima (L), 3 mi. E Kenge (3 ♂, CAS), 13 mi. E Kenge (2 ♀, 1 ♂, CAS), 34 mi. E Kenge (2 ♀, CAS), 21 mi. W Popokabaka (1 ♂, CAS). **Kwilu Province**: 46 mi. W Idiofa (1 ♂, CAS), Ipamu (L), 10 mi. S Lusanga (1 ♀, CAS, as Leverville). **Lomami Province**: Katomba (L), Lusuku (L). **Lualaba Province**: Ditanto (L), Kapanga (L). **Maï-Ndombe Province**: Bena Bendi (L), Bumbuli (L), Tua (L), Lukogi (L), Wamba District: 2 km E Kikongo Mission at 4°16′S 17°12′E (9 ♀, 10 ♂, UCD). **Maniema Province**: Kasongo (L), 62 mi. E Kibombo (1 ♀, CAS), Malela (L). **Mongala Province**: Binga (L). **Nord-Kivu Province**: Walikkale (L) 39 km S Walikale (1 ♀, CAS), 17 mi. W Walikale (1 ♀, CAS). **Nord-Ubangi Province**: Abumombazi (L), Bosobolo (L), Kekongo (L), Yakoma (L). **Oriental Province**: Avakubi at 1°20′N 27°37′E (3 ♂, AMNH), Epulu [River] (1 ♀, 1 ♂, UCD), Mayumbe (L), Zobe in Mayumbe (L). **Sankuru Province**: Komi (L). **Sud-Kivu Province**: Luhoho River at Irangi (1 ♀, CAS). **Tanganyika Province**: 16 mi. SW Kalemie (1 ♂, CAS, as Albertville), Nyunzu (L). **Tshopo Province**: Bafwabaca at 2°10′N 27°0′E (3 ♀, AMNH), Bafwasende at 1°10′N 27°0′E (1 ♀, AMNH), Basoko (L), Bengamisa at 1°0′N 25°10′E (2 ♀, 4 ♂, AMNH), Kisangani at 0°30′N 25°10′E (2 ♀, 20 ♂, AMNH, as Stanleyville), Yangambi (L). **Tshuapa Province**: Bokuma (L), Ikela (L), Lokolenge (L). **Upemba National Park**: Munowe River (1 ♀, CAS).

GHANA: **Ashanti Region**: Akumadan (1 ♂, CAS). **Eastern Region**: Aburi (1 ♂, USNM), New Senchi at 6°12′N 0°05′E (1 ♀, OÖLM).

GUINEA: Mount Nimba National Park at 7°41.66′N 8°24.11′W (3 ♂, OÖLM).

IVORY COAST: **Abijan District**: Abijan: forêt de Banco (1 ♂, CAS), 40 km NW Abijan (1 ♀, CAS). **Lacs District**: Toumodi (♂, CAS).

LIBERIA: **Lofa County**: Voinjama (1 ♂, CAS).

MALAWI: **Northern Region**: Rhumphi (1 ♀, UCD).

MOZAMBIQUE: **Manica Province**: 55 km NW Chimoio at 13°44′S 33°15′E (1 ♂, OÖLM). **Niassa Province**: Cuamba: Mituque Centro Pastoral (1 ♀, OÖLM).

NIGERIA: **Ogun State**: Ikenne at 6°52′N 3°43′E (1 ♀, USNM). **Ondo State:** Ikoya at 6°30′32″N 4°41′28″E (13 ♀, 6 ♂, USNM). **Oyo State**: Olokemeji [Forest Reserve] near Ibadan at 7.42°N 3.55°E (1 ♀, 1 ♂, USNM).

REPUBLIC OF THE CONGO (= Congo Brazzaville): **Cuvette-Ouest:** 15 km S Moyoye at 0°48′41″N 15°23′22″E (1 ♀, OÖLM), Odzala [National Park] (Leclercq, 1969), Oka (1 ♀, USNM). **Pool:** Brazzaville (Leclercq, 1969). **Sangha**: 7 km SW Mokéto at 1°30′14″N 15°54′54″E (1 ♀, OÖLM).

SOUTH AFRICA: **Limpopo**: 35 km W Hoedspruit at 24°23′S 30°40′E (1 ♂, OÖLM).

ZAMBIA: **Central Province**: 60 km NW Kapiri Mposhi (1 ♂, OÖLM). **Copperbelt Province**: 8 mi. SW Ndola (1 ♂, CAS). **Northwestern Province**: 50 km E Mwinilunga (1 ♀, OÖLM), 90 km Solwezi E Chisasa [*sic*] (1 ♂, OÖLM), 100 km W Solwezi at 12°13′S 25°39′E (1 ♀, OÖLM), 150 km W Solwezi: Ntambu at 12°18′S 25°10′E (1 ♂, OÖLM).

ZIMBABWE: **Bulawayo Province**: Bulawayo airport at 20°00′S 28°38′E (1 ♀, 1 ♂, CAS). **Manicaland Province**: Bubi River at 21°42′49″S 30°31′02″E (1 ♂, OÖLM). **Mashonaland West Province**: 30 km W Harare (1 ♀, OÖLM).

Paranysson quadridentatus **(Cameron)**
Figures 45-51.

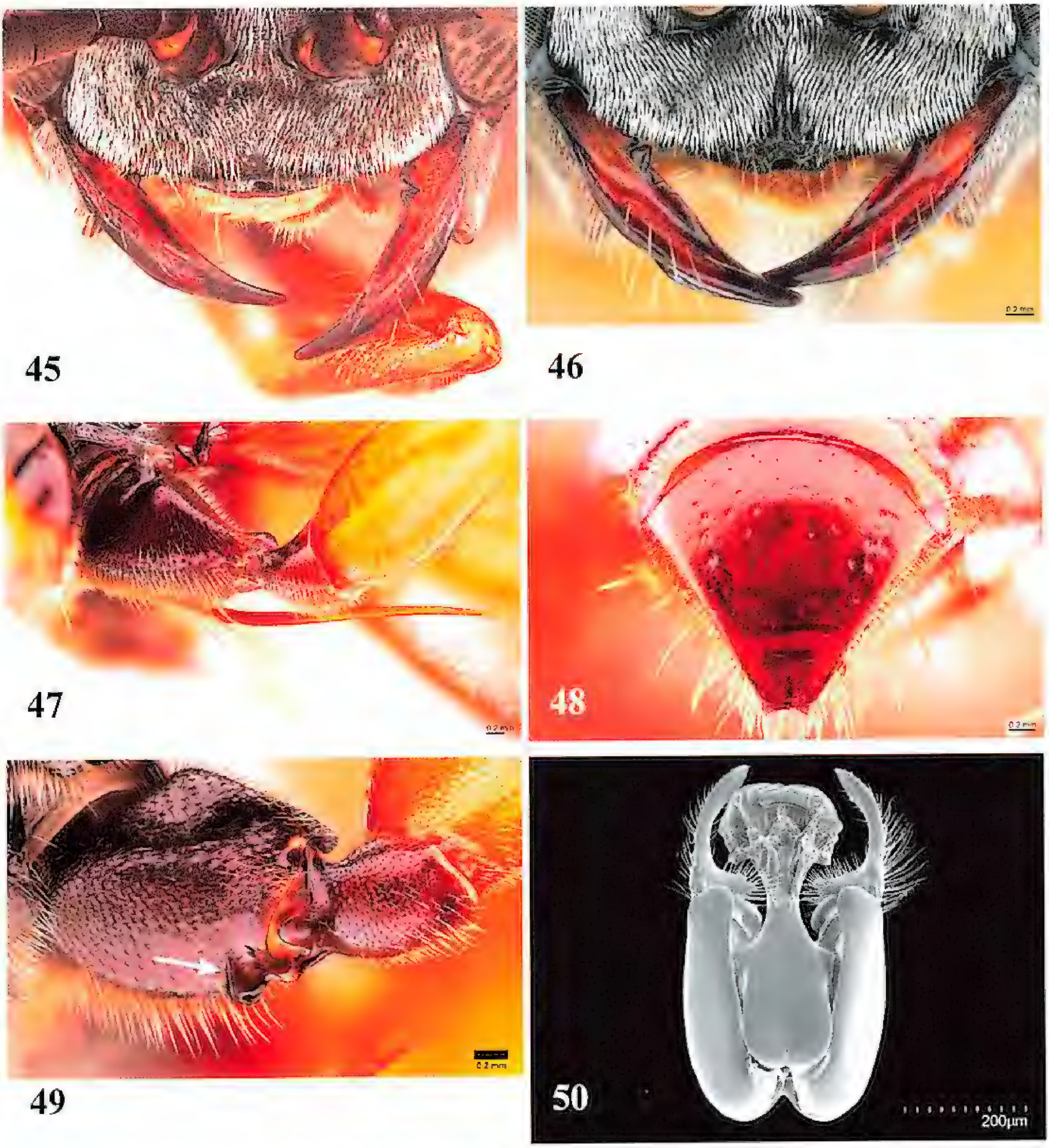
Heliorycetes quadridentatus Cameron, 1910:142, ♀. Holotype or syntypes: ♀, South Africa: Gauteng: Pretoria (TMP), not examined. – Brauns, 1917:242 (type in TMP). – As ***Paranysson quadridentatus***: R. Turner, 1914:340 (new combination, in revision of *Paranysson*); Arnold, 1923:13 (in revision of African *Paranysson*), 1930:7 (in checklist of Afrotropical Sphecidae); Leclercq, 1968:91 (in revision of African *Paranysson*; Zambia, Democratic Republic of the Congo); R. Bohart and Menke, 1976:308 (in checklist of world Sphecidae); Radović, 1985:65 (sting apparatus analyzed).

Species Identification. In his original description of *P. quadridentatus*, Cameron (1910) says that the hindcoxal spine is as long as three-fourths of the length of the coxa, which seems to point to the species later described as *brevispinosus* Arnold. Unfortunately, I was not able to examine the type material of *P quadridentatus* to verify its identity. Arnold (1929), who may have seen it, says that the hindcoxal spine in *P. brevispinosus* is much shorter and less slender than in *P. quadridentatus*, and I accept his interpretation, in agreement with Leclercq (1968).

Recognition. The female of *P. quadridentatus* can be recognized by its thin and long hindcoxal spine (Fig. 47, at least as long as the hindcoxal venter, originating at about half midocellar diameter before the coxal hindmargin, whereas shorter (except in *P. oscari*) or absent in the other *Paranysson*. *Paranysson oscari* differs by several outstanding characters given under that species. The hindcoxal spine is a similar length in many *P. melanopyrus*, but it originates at about the hindcoxal midlength.

In the male, the hindcoxal venter has a semicircular carina next to its apex that delimits a concave, unsculptured, apical area (Fig. 49), a unique such character. Unlike *P. melanopyrus*, the clypeal free margin is gently arcuate mesally, at most with a pair of rudimentary teeth, and the dorsal length of flagellomere I is equal to 1.2-1.6 × that of flagellomere II (rather than 1.0-1.1 ×)

Subsidiary recognition feature of *P. quadridentatus* are: the longitudinal carina between



FIGURES 45-50. *Paranysson quadridentatus* (Cameron). (45) Female clypeus and mandible; (46) Male clypeus and mandible; (47) Female hindcoxa with spine; (48) Pygidial plate of female; (49) Male hindcoxa (arrow shows semicircular carina); (50) Male genitalia in dorsal view.

propodeal side and posterior surface that is broadened at about two thirds of length, but not forming a tooth, the dorsal length of female flagellomere I is equal to 2.0-2.4 × its apical width, and the female pygidial plate is finely, sparsely punctate throughout.

DESCRIPTION. Clypeal lamella either with two teeth on each side, or teeth absent (Figs. 45, 46). Propodeal dorsum reticulate, in many specimens with predominant longitudinal or oblique ridges. Longitudinal carina between propodeal side and posterior surface broadened at about two thirds of length, but not forming tooth.

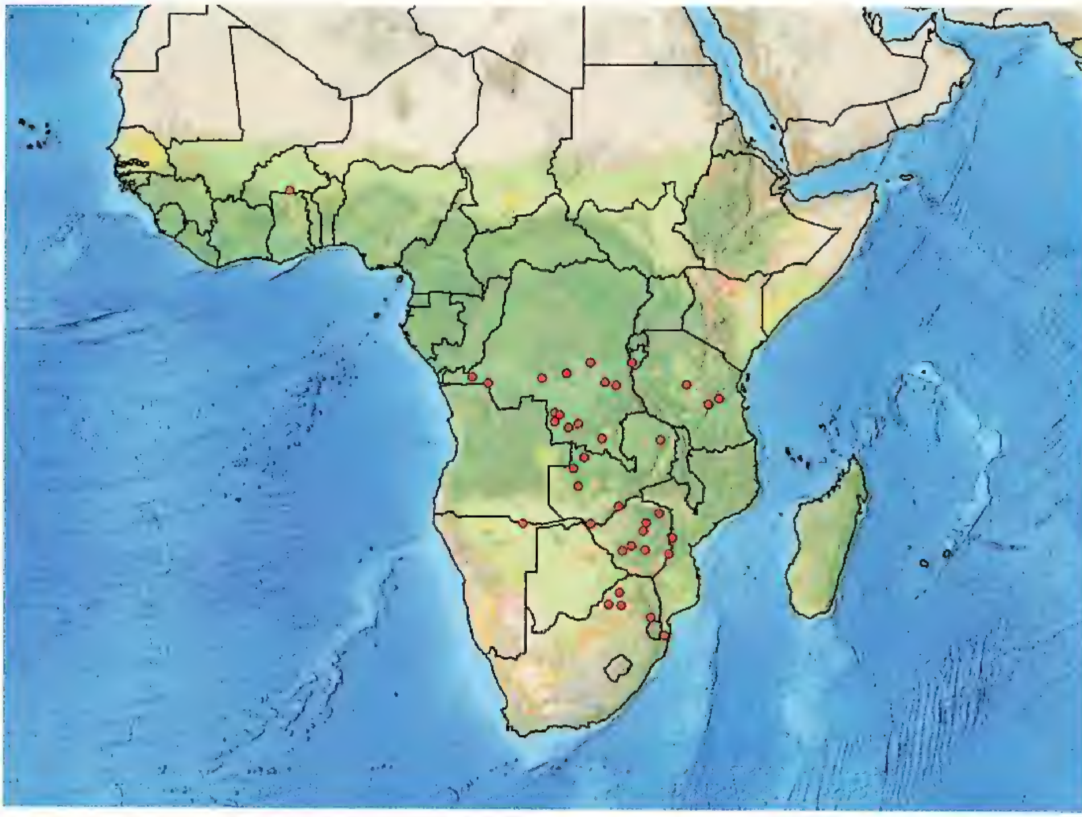


FIGURE 51. Collecting localities of *Paranysson quadridentatus* (Cameron).

♀ – Ocellocular distance equal to 0.8-0.9 × distance between hindocelli; dorsal length of flagellomere I 2.0-2.4 × apical width, of apical flagellomere 1.8-1.9 × its basal width. Hindcoxal spine as long as the hindcoxal venter or longer (Fig. 47). Pygidial plate (Fig. 48) minutely, sparsely punctate throughout (a few punctures may be large). Length 12.9-14.0 mm.

♂ – Ocellocular distance equal to 0.7 × distance between hindocelli. Flagellomere I insignificantly concave ventrally, markedly longer than flagellomere II, its dorsal length 1.4-1.7 × apical width, of apical flagellomere 1.6 × its basal width. Hindcoxa apicoventrally with semicircular carina delimiting concave, unsculptured area (Fig. 49). Terga V-VII closely punctate. Male genitalia (Fig. 50) typical of most species except *P. oscari*. Length 9.6-12.4 mm.

GEOGRAPHIC DISTRIBUTION (Fig. 51). Burkina Faso to South Africa.

RECORDS. **BURKINA FASO: Nahouri Province**: 2 mi. W Pô at 11°11.0′N 1°09.5′W (1 ♂, CAS).

BURUNDI: Rumonge Province: 6 mi. N Rumonge (1 ♂, CAS).

DEMOCRATIC REPUBLIC OF THE CONGO (localities followed by L are from Leclercq, 1968): **Haut-Katanga Province**: Kasenga (L). **Haut-Lomami Province**: Kafakumba (L), Katombe (L). **Kasaï Province**: Luebo (L), Kaolele (L) [province uncertain]. **Kongo Central:** Mayidi (L). **Kwango Province**: Ngowa (L). **Lualaba Province**: Kapanga (L), Tshibalaka (L), Tshibamba (L). **Maniema Province**: 14 mi. W Kibombo (1 ♀, CAS). **Sankuru Province**: 39 mi. NE Lusambo (1 ♀, CAS). **Tanganika Province**: Lukuga River basin (L), Nyunzu (L).

MOZAMBIQUE: Manica Province: 35 km SW Chimoio at 19°08′S 33°09′E (9 ♀, 14 ♂, OÖLM).

NAMIBIA: Kavango-East Region: Rundu (11 ♀, CAS; 4 ♀, OÖLM).

SOUTH AFRICA: KwaZulu-Natal: Tembe Elephant Park at 27°02′S 32°23′E (2 ♀, OÖLM). **Limpopo**: N Modimolle at 24°40′S 28°30′E (1 ♀, OÖLM, as Nylstroom), Thabazimbi (1 ♀, 1 ♂, OÖLM), Waterberg Biosphere Reserve at 23°36′S 28°23′E (1 ♂, OÖLM). **Mpumalanga**: 20 km SE Mbombela (2 ♂, CAS, as Nelspruit).

TANZANIA: Iringa Region: 100 km NE Iringa at 7°37′S 36°17′E (1 ♀, OÖLM). **Morogoro Region**: 62 road km SW Morogoro at 7°02.5′S 37°15.3′E (3 ♀, 2 ♂, CAS). **Singida Region**: 20 mi. SW Itigi (1 (♀, CAS).

ZAMBIA: Muchinga Province: Chipoma Falls at 10°44′58″S 32°0′14″E (2 ♀, 1 ♂, OÖLM). **Northwestern Province**: 150 km S Mwinilunga at 13°11′S 24°14′E (1 ♀, OÖLM), 150 km W Solwezi at 12°18′S 25°10′E (2 ♀, 24 ♂, OÖLM). **Southern Province**: 120 km S Lusaka (2 ♂, CAS; 1 ♀, 8 ♂, OÖLM). **Western Province**: 15 km NW Kaoma (2 ♂, CAS).

ZIMBABWE: Bulawayo Province: Bulawayo: Hillside at 20°12′S 28°37′E (3 ♂, CAS). **Manicaland**: Mount Selinda (1 ♂, OÖLM). **Mashonaland Central Province**: 25 km NE Shamva at Nyagui River (1 ♀, OÖLM). **Mashonaland West Province**: 30 km W Harare (1 ♀, 25 ♂, OÖLM), circa 80 km NE Kwekwe (1 ♀, OÖLM). **Masvingo Province**: Mushandike National Park (1 ♀, 11 ♂, OÖLM). **Matabeleland North Province**: Victoria Falls at 17°56′S 25°50′E (2 ♀, CAS; 2 ♂, USNM). **Midlands Province**: 70 km SW Gweru (1 ♂, OÖLM).

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